Spring 5-13-2017

Population Ecology of Colonially Breeding Seabirds: How Intrinsic Processes, Mediating Influences, and Individual Heterogeneity Affect Population Vital Rates

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POPULATION ECOLOGY OF COLONIALLY BREEDING SEABIRDS: HOW INTRINSIC PROCESSES, MEDIATING INFLUENCES, AND INDIVIDUAL HETEROGENEITY AFFECT POPULATION VITAL RATES

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A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Ecology and Environmental Sciences)

The Graduate School

The University of Maine

May 2017

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Dissertation Co-Advisors: Drs. Cynthia S. Loftin and Shawn T. McKinney

An Abstract of the Dissertation Presented in

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Seabirds have great potential to serve as marine indicators. However, before we can interpret seabird trends with confidence, we need a better understanding of the role of intrinsic processes, mediating influences, and lifetime experience in modulating relationships between prey availability and seabird population dynamics.

Intrinsic processes, mediating influences, and seabird productivity. I assessed productivity (chicks per breeding attempt) at Black-legged Kittiwake *(Rissa tridactyla)* colonies in Prince William Sound, AK and managed Common Tern *(Sterna hirundo)* colonies in the Gulf of Maine. Both systems showed evidence of intrinsic control; factors mediating access to prey were also important.

Mediating influences, individual heterogeneity, and seabird productivity. Productivity integrates events over successive reproductive stages, so events at one stage can modulate the effects of events at other stages. I investigated the effects of individual age and multiple stressors on kittiwake reproduction in Alaska. I found older birds enjoyed greater success across the board, but different external influences drove success at different stages. These results highlight the need to account for both individual heterogeneity and potential interactions among extrinsic processes in interpreting seabird productivity.

Individual heterogeneity and reproductive costs. Reproduction can incur short-term costs in the form of reduced parental survival or breeding activity in the following season. I found evidence of long-term costs in kittiwakes that underwent 0-4 forced nest failures in the early 1990s. Individuals that were forced to fail more were less likely to skip breeding over the following decade, presumably due to associated cost savings. The lack of an observed survival effect suggests that survival is well-buffered in long-lived species, with costs instead borne by parameters less important to lifetime reproductive success.

Intrinsic processes, individual heterogeneity, and seabird survival and recruitment. I investigated the role of colony size in survival, recruitment, and post-recruitment survival of kittiwakes from an Alaskan colony. I found declines in apparent survival associated with increased colony size, likely resulting from increased dispersal of individuals as the colony grew. Recruitment was age-dependent. These results highlight the need to consider intrinsic processes when relating marine bird population dynamics to prey availability and changes in marine ecosystems.

DEDICATION

To my parents, Warren and Kathleen McKnight, for instilling a lifelong love of science and learning, and for attending every science fair, school play, and concert without fail. You have been and always will be my best motivation.

And to my lifelong partner in crime and child-wrangling, Kelsey Sullivan, and Ray and Frank, our own little reproductive successes. Thank you all for your willingness to put up with an absentee mother so that she could pursue her dreams of scholarship. Now we can finally get back to the adventure!

ACKNOWLEDGMENTS

The research reported herein was supported by the U.S. Fish and Wildlife Service's Office of Migratory Bird Management in Anchorage, Alaska; the *Exxon Valdez* Oil Spill Trustee Council; the Earthwatch Institute; the Maine Cooperative Fish and Wildlife Research Unit; the Department of Wildlife, Fisheries, and Conservation Biology at the University of Maine; the Maine Department of Inland Fisheries and Wildlife; the Maine Coastal Islands National Wildlife Refuge; and the National Audubon Society.

My co-advisors Cynthia Loftin and Shawn McKinney were extremely supportive during the development of this project and contributed many valuable insights and suggestions for improving the work. Thanks to them, I complete this degree with a far deeper understanding of ecological problems, science communication, and quantitative techniques than I had when I arrived in Orono.

Collaborating with my committee members has also been an outstanding experience. They have been unfailingly encouraging and their input has greatly improved the quality of both my work and my scientific thought process. I am particularly grateful for their willingness to accommodate my rather ambitious schedule for degree completion.

I want to especially thank David Irons for almost two decades of support and for his extreme patience in enduring shenanigans. I would not have earned this degree were it not for his extraordinary efforts to keep me working in seabird science, even when it meant pushing the employment rules to their limits.

I have received project help in various ways from the following individuals: Andrew Allyn (Gulf of Maine Research Institute), Alex Humphries (Scottish Natural Heritage), Joseph Albanese, Greg Golet (the Nature Conservancy), Linda Welch (Maine Coastal

Islands National Wildlife Refuge), Brad Allen (Maine Department of Inland Wildlife and Fisheries), Sally Sherman (Maine Department of Marine Resources), Steve Moffitt (Alaska Department of Fish and Game), and Grant Humphries (Black Bawks Data Science). Greg Peterson and Bryant DeRoy provided beautiful photography that I have put to use in many presentations and posters.

A special thanks to Karen Lee (George Mason University) who gave a life-changing summer research opportunity to a very unlikely prospect at Connecticut College those many, many years ago. It is you who set me on this long and winding road.

I have much gratitude for the many people who pitched in to help keep my family afloat while I pursued this degree, especially those who watched out for the rugrats and generally helped us to survive while I was busy studenting: Patti and Kerry Sullivan, Brian and Angela Parks, Emily and Chris Genever, Katrina Peterson, April and Greg DaSilva, Sarah and Seth Cottrell, Mikaela and Kevin Wentworth, Scott and Kate Cuddy, Jessica and Scott King, and, of course, Amy Baker.

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CHAPTER 1: GENERAL INTRODUCTION

Human activity disturbs the majority of marine ecosystems around the globe (Halpern *et al.* 2008). The International Panel on Climate Change predicts continued changes in sea surface temperatures, salinity levels, and ocean acidification in response to the rising concentration of greenhouse gases in the atmosphere (e.g., carbon dioxide, methane, and ozone) (IPCC 2007) that will potentially shift species distributions, disrupt predator-prey interactions, impose new physiological constraints on organisms, and alter primary production levels (Sverdup et al. 1942; Mann 1993; Cox et al. 2000, Etherington et al. 2004; Sarmiento et al. 2004). In response, natural resource conservation and management strategies are shifting from species-specific approaches to ecosystem-based approaches and marine spatial planning (e.g., United Nations Educational, Scientific, and Cultural Organization Marine Spatial Planning Initiative, Executive Order No. 13547, Magnuson-Stevens Reauthorization Act 16.US.C. § 1801(3)(3), NOAA Next-Generation Science Plan, U.S. Fish and Wildlife Service National Wildlife Refuge System), yet relationships among organisms and between organisms and their physical environment are not well understood (Weimerskirch et al. 2003; Arkema et al. 2006; Leslie & McLeod 2007). Our limited understanding of complex ecological interactions hinders our assessment of biological dynamics of marine ecosystems and potential effects of large-scale environmental disturbances such as climate change (Griffies 2004).

We have, however, made great strides towards understanding physical and lower trophic level (LTL) ecosystem dynamics in several key marine systems (e.g., the Gulf of Maine; Ji *et al.* 2008). While mid-trophic level (MTL) researchers are making progress toward linking MTL dynamics to physical and LTL models in a few systems (e.g., the

Humboldt Current region; Tam *et al.* 2008), it will likely be some time before MTL modeling is sufficient to support the addition of upper trophic level (UTL) processes (e.g., seabird population dynamics) to complete regional ecosystem models. In the meantime, many UTL researchers, particularly those who study marine birds, have attempted to link apex predator dynamics directly with physics and LTL processes. While these efforts often reveal clear correlations, their interpretations can be uncertain, as these factors are proxies for true predictors, particularly MTL prey availability. As in the childhood game of Telephone, the "message" (i.e., the UTL response) can become more confused with each additional unobserved link between predictor and response.

In this work I take a different approach and focus on *direct* physical and biological linkages to seabird population dynamics, given the current lack of information about prey that is needed to combine seabird modules with LTL modules into complex, cross-trophic level ecosystem models. To that end, my dissertation investigates direct linkages between seabirds and their environment (e.g., nesting habitat and weather), competitors, predators, and prey, while leaving study of factors that indirectly affect seabirds (e.g., chlorophyll and zooplankton dynamics) to others.

I also considered seabird population processes occurring at several different *scales*, another crucial consideration in system modeling. Marine ecosystems are complex, and we know from complex systems science that in such systems, individual-level dynamics often interact to produce emergent population-scale phenomena such as population productivity or growth. Observation scale can therefore shape our perception of these dynamics, potentially leading to very different conclusions depending on that scale. For example, at the population level, reproductive success of seabird cohorts often

increases with age. Individual scale analyses, however, demonstrate that reproductive success may actually remain steady or decline with age (senescent effects), however, mortality of lesser quality individuals over time leaves only the most productive individuals alive as the cohort approaches its maximum lifespan, resulting in the apparent increase in cohort success rate (Aubry *et al.* 2009). Failure to appreciate the individual-scale events that generate such population-scale phenomena can thus lead us to draw erroneous conclusions regarding system dynamics that could hamper attempts to predict system responses to perturbation. Therefore, the more we understand about processes occurring at the individual scale, the better we can model dynamics occurring at higher organizational levels. For this reason, I focused on individual dynamics wherever possible and used individual-scale study subsets to provide context for higher-scale components when possible.

Seabirds have long been recognized for their potential to serve as ecosystem indicators (e.g., Cairns 1987, Piatt *et al.* 2007); population dynamics of these near-apex marine predators integrate the effects of bottom-up ocean processes as well as events occurring at a variety of trophic levels. Seabirds' ability to inform us of forage fish dynamics can be particularly valuable. Collectively, seabirds sample fish stocks over vast areas of the ocean that often are inaccessible to humans, generally preying on understudied fish size classes occurring well before recruitment into commercial fisheries. In comparison to other birds, seabirds employ a conservative, long-lived life history strategy (Weimerskirch 2001). Because this strategy favors "prudent parenthood" that limits reproductive investments in favor of survival (Weimerskirch *et al.* 1995, *but see* Satterthwaite *et al.* 2010), seabird reproductive parameters can be quite sensitive to

local prey abundance (e.g., Suryan *et al.* 2002). This sensitivity is expressed in quantifiable effects that may be easily measured at seabird breeding colonies, thus providing us with a low-cost ecosystem monitoring tool to aid in marine system assessment (e.g., Parsons *et al.* 2008). For this reason, many regions have implemented long-term seabird colony monitoring programs (e.g., *Alaska:* Byrd 2006; *Northwest Atlantic:* Diamond & Devlin 2003; *North Sea:* Frederiksen *et al.* 2004a, *Southern Ocean:* Weimerskirch *et al.* 2003). Further, seabird metrics currently are used in fisheries management in several regions, including the North Sea, the Northwest Atlantic, and the South Atlantic (Einoder 2009).

Before we can interpret seabird trends with confidence, however, we need a better understanding of the role of *intrinsic processes*, *mediating influences*, and *individual heterogeneity* in modulating relationships between prey availability and seabird population dynamics. In the following chapters, I investigate questions pertaining to these three elements. Seabird responses to prey availability may change depending on how close a population is to its carrying capacity, which is determined by a combination of resource limitation (e.g., nest sites), predation, competition, and disease. How influential are these intrinsic processes? Seabird responses also can be mediated by environmental factors (e.g., weather that interferes with foraging) that alter their ability to react to changes in prey. Which of these mediating factors is important to consider in population modeling? Differences in quality and life experience can also shape individual relationships to prey, and differences in individual response can scale up to have surprising implications at the population level. How can these individual differences modify seabird/prey relationships?

The goal of my dissertation was to investigate the major influences on seabird reproductive success, survival, and recruitment. Although this dissertation is subdivided into four discrete project components or chapters, the themes discussed in this introduction appear as common threads throughout. My focal populations were Black-legged Kittiwakes *(Rissa tridactyla)* in Prince William Sound, Alaska (chapters 2 – 5), and Common Terns *(Sterna hirundo)* in the Gulf of Maine (chapter 5). Ultimately, each project element contributes a new piece of information to the effort to understand, model, and manage seabird dynamics in complex marine systems. As a whole, this work highlights the need for continued monitoring of seabird populations coupled with directed investigations that can quantify the links between mediating environmental influences, intrinsic processes, individual experiences and seabird population dynamics on a larger scale.

CHAPTER 2: COMMON THREADS IN SEABIRD PRODUCTIVITY PATTERNS ACROSS TWO SYSTEMS

ABSTRACT

Reproductive success at seabird colonies is often quite variable, even within a single region. Although exhaustive investigations of reproductive success drivers are not logistically feasible, many long-term seabird colony monitoring datasets may be combined with ancillary environmental datasets to reveal key relationships that may inform management and future investigations. Here we explored biological and environmental influences on reproductive success of two surface-feeding seabird species (Black-legged Kittiwakes *Rissa tridactyla* and Common Terns *Sterna hirundo*) that inhabit different oceans and climate zones and experience different management approaches; the terns' predators were controlled while the kittiwakes were not managed. Both systems showed evidence of negative density dependence between colony size and reproductive success, contrasting with positive associations between region-wide population density and reproductive success. Direct environmental influences were also important productivity drivers; milder summer winds and greater median depth in colony foraging range were associated with greater productivity in both systems. Kittiwake productivity also was affected by precipitation (-), local herring spawn activity (+), and predation (-), while tern productivity increased with spring sea surface temperature. Kittiwakes also exhibited a contrasting effect of colony size on the probability of colony success, where large colonies were less likely to fail entirely, but among productive colonies, size was negatively associated with reproductive success. Understanding the

complex factors contributing to seabird reproductive success will supply valuable context for our interpretations of seabird demographic patterns and inform colony management response to environmental change.

INTRODUCTION

Seabirds have long been recognized for their potential to serve as ecosystem indicators (e.g., Cairns 1987, Piatt *et al.* 2007). Collectively, seabirds effectively sample fish stocks, often at life stages occurring well before recruitment into commercial fisheries, over vast areas of the ocean. In comparison to other birds, seabirds employ a conservative, long-lived life history strategy (Weimerskirch 2001). Because this strategy favors "prudent parenthood" that limits reproductive investments in favor of survival (Weimerskirch *et al.* 1995, *but see* Satterthwaite *et al.* 2010), seabird reproductive parameters can be quite sensitive to local prey abundance (e.g., Suryan *et al.* 2002). This sensitivity is expressed in quantifiable effects that may be easily measured at seabird breeding colonies, thus providing us with a low-cost ecosystem monitoring tool to aid in marine system assessment (e.g., Parsons *et al.* 2008). For this reason, many regions have implemented long-term seabird colony monitoring programs (e.g., *Alaska:* Byrd 2006; *Northwest Atlantic:* Diamond & Devlin 2003; *North Sea:* Frederiksen *et al.* 2004a, *Southern Ocean:* Weimerskirch *et al.* 2003). Further, seabird metrics currently are used in fisheries management in several regions, including the North Sea, the Northwest Atlantic, and the South Atlantic (Einoder 2009).

Connections between prey and seabird reproductive success have been well-documented. Evidence for these linkages stems from both (A) direct studies of diet

influence on seabird reproduction (e.g., Wanless *et al.* 2005, Hatch 2013, Kowalczyk *et al.* 2014, Renner *et al.* 2014), and (B) identification of associations between fish stock fluctuations and seabird breeding metrics (e.g., Croll *et al.* 2006, Davoren & Montevecchi 2003). The latter relationship may be more elusive, as seabirds have biological and behavioral buffering capacities to compensate for reduced prey availability (e.g., Suryan *et al.* 2000). Therefore, the response may be most evident when food is scarce (i.e., less than one-third of the maximum regional forage fish biomass; Cury et al. 2013).

Given seabird buffering capacity, we might expect that when food availability is above the seabirds' compensable threshold, we would see consistently high reproductive success at seabird colonies. Instead, seabird success can be quite variable, even when regional prey abundance appears adequate (e.g., Jodice *et al.* 2006). Clearly, other factors also affect seabird reproductive success. These can act through direct effects on nestlings (e.g., *weather:* Threlfall *et al.* 1974, *predators:* Pascal *et al.* 2008), phenology (e.g., Ramos *et al.* 2002, Reed *et al.* 2006), and foraging success (e.g., Finney *et al.* 1999). It is important to consider such factors when we interpret seabird colony dynamics with respect to marine system dynamics, as reduced fledgling production may result directly from forage fish stock depletion or from other factors entirely.

Although it is neither financially nor logistically feasible to simultaneously monitor all factors potentially affecting seabird reproduction, we can use existing data to increase monitoring efficiency. There is a wealth of archived seabird monitoring data that may be combined with independent ancillary datasets (e.g., fish stocks, environmental variables) to offer insight into factors important to seabird reproduction. Here we

investigate multiple seabird colonies within two systems in which reproductive success is variable but regional prey abundance generally is not depleted beyond the one-third maximum biomass threshold identified by Cury *et al.* (2013). We explore two questions: 1) What factors relate to fluctuations in seabird reproductive success, and 2) do these factors vary between our focal species and regions? We used archived seabird monitoring data for Black-legged Kittiwakes (*Rissa tridactyla;* 'kittiwake' hereafter) and Common Terns *(Sterna hirundo;* 'tern' hereafter) in combination with independently collected datasets on prey, competitors, habitat, weather, and climate to build and compare mixed effects models in order to identify drivers of seabird reproductive success. We sought to identify associations between seabird reproductive success and factors that may affect it such as food availability, intrinsic processes, environmental conditions, and predation.

METHODS

Focal species

The Black-legged Kittiwake is a small surface-feeding gull with a circumpolar range. Kittiwake monitoring programs occur throughout the species' range, including on colonies in France (e.g., Aubry *et al.* 2011), the U.K. (e.g., Wanless *et al.* 2007), Canada (e.g., Regehr *et al.* 1997), and Alaska (Dragoo *et al.* 2012). Kittiwakes are largely piscivorous, forage in both nearshore and pelagic habitats, and feed their chicks via regurgitation. Pacific herring *(Clupea pallasii)* and Pacific sand lance *(Ammodytes hexapterus)* are important components of kittiwake diet in Prince William Sound, AK (Suryan *et al.* 2002).

Common terns are surface feeders with a temperate-subarctic circumpolar distribution in the northern hemisphere, though they are absent from the northeast Pacific. Breeding colonies have been continuously monitored in coastal areas for many years throughout the terns' range, most notably in the U.S. (e.g., Nisbet & Cam 2000) and Germany (e.g., Becker *et al.* 2001). Terns forage primarily nearshore, though they forage offshore as well (Nisbet 2002). Unlike kittiwakes, terns carry chick meals in their bills, which limits meals to cohesive prey types such as fish and large macrozooplankton. Within the Gulf of Maine, Atlantic herring *(*Clupea harengus*)* and white hake *(Urophycis tenuis)* generally constitute the majority of chick diets (Hall *et al.* 2000).

Site descriptions

Prince William Sound ('PWS' hereafter) is an estuarine embayment (~ 10,000 km^2) in the northern Gulf of Alaska, centered at roughly 60º N 147ºW (Fig. 2.1a) and bordered by the Chugach and Kenai Mountains (up to 4km elevation), which contribute to ~6,000 km of rugged coastline. The system is characterized by numerous deep fjords, rocky islands, and glaciers (26 tidewater glaciers and many alpine glaciers; Lethcoe 1987) that supply freshwater runoff to this marine system. Water circulation is dominated by the Alaska Coastal Current (ACC), which mixes with a large volume of fresh water input from precipitation, rivers, and glaciers. Westerly and southwesterly currents predominate with a branch of the ACC entering through the eastern entrance, crossing PWS from east to west before exiting through the western strait (Nibauer *et al.* 1994). Strong tidal currents with a tidal range up to six meters cause rapid mixing of waters at

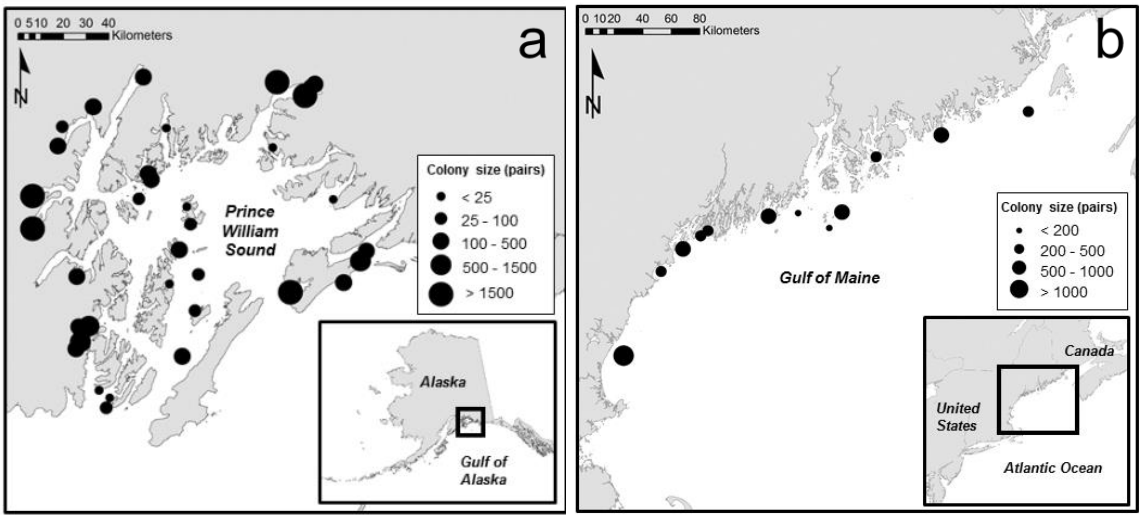

Figure 2.1. Colony locations. Black-legged Kittiwake colony locations in Prince William Sound, AK (a) and managed Common Tern colonies in the Gulf of Maine (b). Circle sizes represent average colony sizes during active years. Inset depicts locations within the broader regions.

the entrances to bays, fjords and inlets. During the winter, ice forms at the heads of protected bays and fjords that receive substantial freshwater runoff (Isleib & Kessel 1973). This dynamic environment makes PWS an extremely productive system, providing for a rich and complex food web. PWS was the site of a large oil spill in 1989 when the tanker *Exxon Valdez* ran aground on Bligh Reef in the northeastern Sound, spilling an estimated 11 million gallons of oil into PWS and triggering a massive multi-year cleanup effort.

PWS generally hosts ~20,000 breeding kittiwakes nesting at more than two dozen black-legged kittiwake colonies, though the exact number of colonies fluctuates (Fig. 2.1a). Most colonies are located on rocky coastal or island cliffs, and several regularly number more than 5,000 breeding birds, although most are considerably smaller. Colonies are primarily monospecific, though Glaucous-winged gulls *(Larus glaucescens)* often nest around the edges or on top of kittiwake colony cliffs and a few colonies

sometimes have small numbers of double-crested cormorants (*Phalacrocorax auritus*) nesting among them.

The Gulf of Maine ('GOM' hereafter) is a large estuarine-influenced embayment (93,000 km^2) bordered by New England and southeastern Canada and partially separated from the Atlantic Ocean by shallow underwater banks. The GOM has an average depth of 150 m (Thompson 2010) and 17,000 km of coastline. The Gulf of Maine circulation is characterized by cyclonic gyres in the deep interior basins, anticyclonic gyres over shallow banks, including Georges Bank, and a southwestward Gulf of Maine Coastal Current in two parts, the East Maine Coastal Current and West Maine Coastal Current (Brooks 1985, Pettigrew *et al.* 2005). Tidal mixing is particularly strong in the eastern GOM where tidal effects are concentrated by the funnel-shaped Bay of Fundy.

As of 2013, 40,000 Common Terns bred on 13 managed islands (including Monomoy Island south of Cape Cod; not included in this study) and several unmanaged islands in the Gulf of Maine (Fig. 2.1b). Managed islands host multiple species, including Arctic *(S. paradisaea)*, Roseate *(S. dougallii),* and Least Terns *(*Sternula antillarum*),* Atlantic puffins *(Fratercula arctica)*, and Razorbills *(Alca torda)*; Common Tern numbers at each colony range from 200 – 15,000 breeding pairs (GOMSWG 2013). Management techniques vary among islands but generally involve a combination of predator control and vegetation management.

Field data collection

KITTIWAKES -- During 1985-2012, co-author Irons visited each known kittiwake colony in PWS twice annually to document breeding effort (i.e., number of nests built)

and productivity (i.e., near-fledging chicks produced per nest built). These counts included all nests and chicks at each colony, therefore providing actual population values rather than representative values from sampled subsets, though most colonies were subdivided into breeding plots delineated by easily recognizable features of the cliff face. In late May to early June, when birds had begun incubation, Irons counted all nests by plot on all faces of the colony with 10 X 42 binoculars from an 8 m Revenge class Boston Whaler. We used these values to represent colony size (number of breeding pairs), eliminating (1) colony-years if no pairs attempted nesting, and (2) any colonies from the analysis that never exceeded 50 breeding pairs, because such small, ephemeral colonies were apt to go undetected elsewhere and thus may not have been well-represented. Irons returned to each colony in late July to early August (close to fledging) to count the number of single, double, and triple chick nests using the same method as before. We calculated productivity (number of chicks/nest) for each colony by dividing the number of chicks observed during the second visit by the number of nests counted in the first visit.

To characterize predation, we also calculated the population level coefficient of variation in brood size at fledging for each colony with >1 subplot, under the premise that (A) predation reduces the brood size of some, but not all nests in a colony, as predators tend to target specific nesting patches first, then systematically work outward from there (Robbins 2009, unpublished US FWS data); and (B) predation affects plots less uniformly than food limitation. Variation in brood size should thus correlate inversely with predation pressure (so long as colonies do not experience very high levels of predation where most nests fail), as high predation rates mean more equal numbers of

failed (brood size = 0) and successful (brood size ≥ 1) nests. Indeed, we found that the coefficient of variation had a slightly negative relationship with productivity, supporting the premise that it was not a direct component of productivity and was a reasonable proxy for predation pressure (see the results for more on this relationship).

TERNS – Observers (U.S. Fish and Wildlife Service, Maine Coastal Islands National Wildlife Refuge and the National Audubon Society) have documented annual tern productivity in 12 managed GOM colonies since 2001 by monitoring colony plots representing ~5% of the breeding population. Plots were generally fenced off and contained 5-10 nests each. Nest contents were examined daily during incubation and every two days following hatch. Chicks were assumed to have successfully fledged if they remained in the nest area for at least 15 days following hatching. Productivity values were calculated for each plot within a colony, then averaged over plots to give the mean colony productivity (USFWS 2014).

Colony sizes were estimated in an annual nest census conducted early in the incubation period (May). In the weeks prior to the census, crew members attempted to identify and mark ~20% of tern nests to species through a combination of blind and incidental observations in high, medium, and low nesting density areas. During the census, all detected nests were marked. Later on the same day, surveyors searched transect lines through the surveyed area to count nests that had been missed during the initial survey; the ratio of marked to unmarked nests was used to develop and apply a Lincoln index correction factor (Bibby *et al.* 1992) to the original survey results. The species ratio was then applied to the corrected nest count to estimate the number of nests

belonging to each species (USFWS 2014). We eliminated colony-years from the analysis if no pairs attempted to nest. We did not compute a predation metric for terns because predators are controlled at managed colonies.

Defining colony foraging ranges

We used ArcMap (v. 10.4; ESRI, Inc.) to define a foraging area for each colony as the area within 45 km (the maximum average annual forage range documented by Ainley *et al.* 2003) overwater distance of each kittiwake colony and within 20 km of each tern colony (Nisbet 1983) using coastline shapefiles for each region (PWS: G. Drew, U.S. Geological Survey; GOM: NOAA 2014). We defined kittiwake range by overwater distance, because much of the land mass in PWS is mountainous and serves as a travel barrier for seabirds, rendering overland flights between fjords extremely unlikely. We extracted precipitation and habitat data from within these areas and associated them with the corresponding colony (see below). We also calculated the total water area within each colony's foraging range, the total shoreline area ($\leq$ 400 m from land), and the ratio of the shoreline area to the total area within each foraging range. Spatial data were projected into the Alaska Albers equal area conic (PWS) or the Lambert conformational conic coordinate systems (GOM) prior to any geographic analysis.

Inter-colony competition

We calculated annual potential population densities in each colony's foraging range as an index of inter-colony competition based on colony sizes associated with any overlapping foraging ranges to characterize possible inter-colony competition. We first

identified all overlap regions between each colony pair with the Intersect tool in ArcMap 10.1 (ESRI 2011). We then assigned all associated colony names to each intersected polygon segment with the Polygon Neighbors tool. Assuming a uniform distribution of birds within each colony's foraging range, we calculated the number of birds theoretically occupying each intersected segment, and used these values to calculate a total population density within each colony's foraging range.

Ancillary datasets

We incorporated a number of metrics derived from ancillary datasets in our modeling process, including metrics associated with bathymetry, precipitation, wind, sea surface temperature (SST), climate, prey availability, and interspecific competition (Tables 2.1, 2.2, A1, A2). We extracted bathymetry raster values (PWS: Caldwell *et al.* 2011; GOM: Banner 2002) contained within each colony's foraging range and then calculated the average and median depths and amount of "shallow" habitat (PWS: ≤30 m, GOM: ≤18.3 m; cutoff values dictated by depth categories as defined in each bathymetry dataset). We extracted modeled daily precipitation data (Thornton *et al.* 2016) for the geographic coordinates of each colony and computed the number of days when precipitation (mm) exceeded 0 and 15, as well as the total precipitation for June and July. The resolutions of modeled monthly wind (m/s; u and v vectors; Kalnay *et al.* 1996, ESRL 2016a) and SST (ESRL 2016b) were too coarse to allow for colony-specific value extraction. Instead, we extracted a single value of each variable and region (PWS: 60.0° N, 147°W; GOM: 42.5° N, 67.5°W) corresponding to July (winds) and May (SST). We also computed the absolute value for E/W and N/S winds as well as the overall wind

Table 2.1. Ancillary datasets. Ancillary dataset source, resolution, description, and time period used to model productivity in (1) Black-legged Kittiwakes in Prince William Sound (PWS), AK, and (2) Common Terns in the Gulf of Maine (GOM).

Variable group (region)	Source	Resolution	Description	Time period
Depth (PWS)	Caldwell et al. 2011	8 arc-seconds	Mean higher high water digital elevation map	NA
Depth (GOM)	Banner 2002	1:24,000 inshore 15 second offshore	Raster of bathymetry and intertidal cover types	NA
Precipitation (both)	Thornton et al. 2016	1 km	Daymet Version 3 model precipitation output	1985 - 2015
Wind (both)	ESRL 2016a	T62 Gaussian grid 192 X 94	NCEP/NCAR Reanalysis Monthly Means for u- and v-winds	1985 - 2015
SST (both)	ESRL 2016b	T62 Gaussian grid 192 X 94	NOAA Optimum Interpolation Sea Surface Temperature V2	1985 - 2015
Nino 3.4 (both)	ESRL 2016c	Non-spatial	Index based on area-averaged SST from 5S-5N and 170-120W	1985 - 2016
PDO (PWS)	JISAO 2016	Non-spatial	Index derived from OI.v2 SST fields	1985 - 2016
NAO (GOM)	NWS-CPC 2016	Non-spatial	Multivariate teleconnection index	1985 - 2016
AMO (GOM)	ESRL 2016d	Non-spatial	Index calculated from Kaplan SST dataset;	1985 - 2016
Fish (PWS)	Moffitt 2016	50m	Digitized linear representations of herring milt observed during aerial surveys	1985 - 2012
	HRMT 2014	Non-spatial	Rebuilt PWS herring age-structure-analysis/Bayesian framework	1985 - 2011
	Moffitt, pers. comm.	Non-spatial	Hatchery-reared salmon parr released by	1985 - 2012
	Sheridan et al. 2014	Non-spatial	Salmon landing and escapement reports by management district	1985 - 2012
Fish (GOM)	Sherman, pers. comm.	2km	Maine-New Hampshire Inshore Trawl Survey catch data	2001 - 2016

magnitude. Additionally, given the importance of southwest (upwelling) winds in the GOM, we extracted wind direction and speed for May and June in the GOM and computed southwesterly wind magnitudes for all three months. We also included several indices quantifying regional climate effects to represent potential shifts in large-scale weather patterns that may influence seabirds: the average Niño 3.4 index value (ESRL 2016a) for the preceding December – February (both regions), and individual April – May index values of the sample year for the Pacific Decadal Oscillation ("PDO" hereafter; PWS; JISAO 2016), the North Atlantic Oscillation ("NAO" hereafter; GOM; NWS-CPC 2016), and the Atlantic Multidecadal Oscillation ("AMO" hereafter; GOM; ESRL 2016d).

We represented fish prey (herring) and interspecific competition (*PWS:* salmon; GOM: silver hake, sculpin) with archived fish survey datasets. In PWS, where age class 0 and 1 herring are important components of the kittiwake diet (Suryan *et al.* 2000) we used aerial surveys of spring herring spawning activity (Moffitt 2016) to extract the number of cells (100 m^2) representing herring spawning activity within each colony's foraging range. We applied this metric in two ways. First, we related it to the following year's kittiwake productivity as an index of availability of age-1 herring availability, assuming that larvae are retained within nursery habitats (e.g., McGurk *et al.* 1993) so that age-1 abundance is correlated with spawn production in the previous year. Second, we related it to the current year's kittiwake productivity as an index of age-0 herring availability. We also connected the modeled number of age three herring from a PWS age-structure-analysis (HRMT 2014) to kittiwake productivity two years prior – a more defensible but non-spatially explicit alternative to representing age-1 herring abundance (prey). Although salmon are not a large component of kittiwake diets in PWS (Dragoo *et al.* 2012), kittiwakes are known to feed on hatchery-reared salmon fry in this region (Scheel & Hough 1997). Therefore, we also included the annual number of hatchery-reared parr (age-1 and combined age-1 and age-2) released within each colony's fishery management subdistrict (N=20) as potential prey variables. Because kittiwakes likely compete with salmon for food (Springer & van Vliet 2014), we used an estimate of adult salmon density by summing adult salmon landings and escapement for each subdistrict (Sheridan *et al.* 2014) and calculating an estimated adult salmon density for each colony's foraging range using the same technique we employed to compute seabird population densities within those ranges.

In the GOM, we calculated a number of potential prey and competitor metrics from catch data collected during the fishery-independent Maine-New Hampshire Inshore Trawl Survey (for data collection methodology, see Chen *et al.* 2006; data provided by S. Sherman, *pers. comm.*). The trawl sampling area aligned with seabird foraging ranges, with an average of 5.7 ± 0.3 (95% CI) 1 nautical mile tows within each colony's foraging range in each year. Limiting the chick meal prey length to < 140 mm (Nisbet 2002), we calculated the average number of prey-sized Atlantic herring and silver hake *(*Merluccius bilinearis*)* per tow within each colony's foraging range. We also calculated the average number of herring and hake >140 mm per tow (reflecting potential competitors).

Mixed effects modeling

We performed several data management tasks to optimize modeling effectiveness. First, we z-standardized all covariates to facilitate interpretation of relative effect sizes. Second, we addressed missing data values using one of two approaches. For annual datasets missing a single year, we replaced missing values with 0s, the center of the z-standardized distribution, so that we could model the effects of remaining covariates on productivity in those years with minimal influence from the replaced value. In years with many missing values, we restricted the analysis to only those records with complete data. For this reason, we modeled tern productivity only during 2001 - 2016, the years when fish data were available, despite availability of seabird productivity monitoring data in previous years.

We used the *glmer* and *lmer* functions from the lme4 library (Bates et al. 2014) in Program R (R Core Team 2016) to build mixed effects models investigating relationships

between kittiwake and tern productivity and colony size, inter-colony competition, depth, foraging area, precipitation, wind, SST, and climate variables. Because the kittiwake colony productivity distribution was heavily zero-inflated, we were unable to identify a single response distribution that allowed models to meet residual assumptions. We therefore used a two-stage approach for the kittiwake analysis: (1) we used a binomial distribution in generalized linear mixed effect models to investigate factors contributing to the probability of a colony producing any chicks at all (reproductive success); (2) we modeled only positive productivity values in linear mixed effects models to examine what factors are associated with varying degrees of colony-level reproductive success (reproductive output, given success). For the latter, we employed a Gaussian distribution with a fourth-root response transformation to meet model assumptions. Tern colony productivities were also right-skewed; however, there were insufficient 0 values (N=23 of 255 records) to model binary reproductive success separately. We therefore modeled only reproductive output, given success, for terns with a Gaussian distribution. During each model run we evaluated top model residual distribution, normality, and dispersion (for generalized linear mixed models) to assess whether model assumptions were met. If residuals were sufficiently homoscedastic and normally distributed, or if not normally distributed, at least not over-dispersed, we accepted the model fit as sufficient.

Modeling approach

Prior to multi-variable modeling, we identified the best representative metric within each category of potential predictors (e.g., wind metrics) by building and comparing single variable models with AIC model selection. We then combined the best-

performing metrics from each variable group to build a global model. We did not include combinations of strongly correlated metrics ($r \geq 0.70$ or $r \leq -0.70$) in global models. If the global model failed to converge, we sequentially dropped the variables from the single variable models with the highest AIC scores until convergence was achieved. We then tested for the ability of each variable to improve the model by comparing model performance, via AIC score, of the global model versus the model with each individual variable removed. Variables whose omission worsened the AIC score by more than two AIC units ("key variables") were included in the final model. For variables whose omission worsened the global model's AIC score by less than two AIC units, we assessed their relative contribution by (1) performing an analysis of variance (ANOVA) between the global model and the model missing the variable in question and (2) building and comparing AIC values for additive models of key variables both including and excluding the variables in question. If more than one key variable model was competitive (i.e., within 2 AIC units of the top-scoring model), we evaluated support for retaining the additional variable via an ANOVA comparison.

Validation

The kittiwake dataset was sufficiently large (N = 616 colony-years) to randomly select and retain a quarter of the records (N=154) for model validation. We were therefore able to evaluate the performance of the top kittiwake model from each stage by predicting productivities for held out records using top model coefficients. For the reproductive success analysis, we iteratively determined the probability threshold value (to the nearest 0.01) that balanced the proportions of correctly predicted successes and

failures. For the analysis of reproductive output, given success, we evaluated the model's predictive capability by regressing observed values on fitted values and assessing both the R^2 value and the deviation of the regression line from the ideal fit line y=x.

RESULTS

PWS kittiwakes

We found no relationship between the brood size coefficient of variation and colony size (slope = 0.002, R^2 = 0.0009). The population standard deviation of brood size among plots increased with productivity (slope = 0.34, R^2 = 0.28), as expected, given that brood size is bounded by 0, restricting variability at the low end of the variable's range. Productivities rarely approached the theoretical maximum, allowing for greater variability at the high end. The average coefficient of variation in brood size at fledging for all productive colonies was 1.22 ± 0.03 (95% confidence interval).

Reproductive success was poorer when the foraging range was shallow, the colony size was small, and N/S winds were heavy (Table 3). We modeled the probability of kittiwake chick production in PWS with 462 observations from 39 colonies active during at least part of 1985 - 2012, representing 262 successes and 200 failures (zero chicks produced). The top-ranked single variable model explaining colony-level reproductive success included only colony size as a fixed effect and both colony and year as random effects (Table A3). The multi-variable selection process favored the retention of only the colony size, wind, and depth variables (Table A4).

Among successful kittiwake colonies, reproductive output was poorer when inter-colony comptition was low, rain was plentiful, herring spawning was reduced, colony

size was large, and predation pressure was high (Table 3). We modeled reproductive output, given success, for the 262 records with positive productivity values using a Gaussian distribution with a transformed response (0.4 power) and colony and year as random effects. The top-ranked single variable model explaining kittiwake reproductive output included only brood size variability as a fixed effect; the second best-performing model included only inter-colony competition (ΔAIC = 134.82; Table A5). The multiple variable selection process favored the retention of the predation, inter-colony competition, rain, herring spawning stock, and colony size variables (Table A6). A regression of observed values from the training dataset on fitted values using the top model coefficients had a slope of 1.2, evidencing an increasing tendency toward underestimation at larger values, and an adjusted R^2 value of 0.53 (Fig. A1).

Table 2.2. Productivity modeling metrics. Metrics used in modeling productivity for Black-legged Kittiwakes in Prince William Sound (PWS), AK, and Common Terns in the Gulf of Maine (GOM). One representative variable from each group was selected for multi-variable modeling based on performance in single-variable mixed effects models explaining seabird productivity. *Table continued on following page.*

Variable group	Metrics used in modeling
Colony size (both)	Number of breeding pairs at each colony in each year
Inter-colony competition	Density of individuals from all colonies combined within a colony's foraging area
Brood size variability (supplemental PWS)	Coefficient of variation in average brood size at fledging over plots at colony site
Area (both)	Total area of colony foraging range Total shoreline area (≤400m from land) within colony foraging range Ratio of shoreline to total area of colony foraging range
Depth (PWS)	Mean depth within foraging range of colony Median depth within foraging range of colony Number of raster points (0.12km) representing depth ≤30m within foraging range of colony
Depth (GOM)	Mean depth within foraging range of colony Median depth within foraging range of colony Number of raster points (0.025km) representing depth ≤18.3m within foraging range of colony
Precipitation (both)	Total June precipitation (mm) at colony site Number of June days with precipitation > 0mm at colony site Number of June days with precipitation > 14mm at colony site Total July precipitation (mm) at colony site Number of July days with precipitation > 0mm at colony site Number of July days with precipitation > 14mm at colony site
Wind (both)	Average July wind magnitude (one value for the region) Average directional July N/S wind (one value for the region) Average July N/S wind magnitude (one value for the region) Average directional July E/W wind (one value for the region) Average July E/W wind magnitude (one value for the region)

Table 2.2 continued.

Variable group	Metrics used in modeling
Wind (GOM)	Average May NE wind magnitude (one value for the region) Average June NE wind magnitude (one value for the region) Average July NE wind magnitude (one value for the region)
SST (both)	Modeled mean May sea surface temperature (one value for the region)
SST (GOM)	Modeled mean June sea surface temperature (one value for the region) Modeled mean July sea surface temperature (one value for the region)
Nino 3.4 (both)	Average December-February ENSO Nino 3.4 index value (one value for the region)
Pacific Decadal Oscillation (PWS)	April Pacific Decadal Oscillation index value (one value for the region) May Pacific Decadal Oscillation index value (one value for the region) June Pacific Decadal Oscillation index value (one value for the region) July Pacific Decadal Oscillation index value (one value for the region)
North Atlantic Oscillation (GOM)	April NAO index value (one value for the region) May NAO index value (one value for the region) June NAO index value (one value for the region) July NAO index value (one value for the region)
Atlantic Multidecadal Oscillation (GOM)	April AMO index value (one value for the region) May AMO index value (one value for the region) June AMO index value (one value for the region) July AMO index value (one value for the region)
Fish (PWS)	Number of herring spawn points within foraging range of colony Modeled number of age 3 herring (one value for the region) Number of age 1 salmon released in colony subdistrict Number of age 1 and age 2 salmon released in colony subdistrict Adult salmon density within foraging range of colony
Fish (GOM)	Frequency of herring with length < 140 mm per tow within foraging range of colony (~prey) Frequency of herring with length >140 mm per tow within foraging range of colony (~competition) Frequency of silver hake with length < 140 mm per tow within foraging range of colony (~prey) Frequency of silver hake with length > 140 mm per tow within foraging range of colony (~competition) Frequency of combined herring and silver hake with length < 140 mm within foraging range of colony (~prey) Frequency of combined herring and silver hake with length > 140 mm within foraging range of colony (~competition)

Validation

The validation dataset for the top-ranked stage one binary model consisted of 154 held out records including 79 successes and 75 failures. Prediction was best using a cutoff of 0.58 (predicted success probability of 0.58 or greater = "success"; less than 0.58 = "failure"). Using this cutoff value, 73% of successes, 75% of failures, and 74% of overall outcomes were correctly predicted by the top model.

The validation dataset for the top ranked stage two kittiwake productivity model consisted of 76 records. A regression of observed on fitted productivity values had a slope of 1.33, indicating an increasing tendency toward underestimation at larger values, and an adjusted R^2 value of 0.41 (Fig. A2).

GOM terns

Tern productivity was poorer when inter-colony competition was low, May SST was cold, the average foraging range depth was shallow, June northeast winds were strong, and colony size was large (Table 2.3). We modeled tern productivity for the 172 records with positive productivity values with colony and year as random effects. The top-ranked single variable model explaining tern productivity included only inter-colony competition as a fixed effect (Table A7). During the multivariable analysis, the selection process favored retention of inter-colony competition, SST, depth, wind, and colony size (Table A8). A regression of observed values on fitted values for the top model had a slope of 1.27, indicating an increasing tendency toward underestimation at larger values, and an adjusted R^2 value of 0.34 (Figure A3).

Table 2.3. Top model coefficients. Fixed effect coefficients from the best performing models describing the probability of chick production at Black-legged Kittiwake colonies in Prince William Sound, AK during 1985 – 2012 (top left), Black-legged Kittiwake productivity in Prince William Sound, AK, during 1985-2012 (bottom left), and Common Tern productivity in the Gulf of Maine during 2001-2016, all with both colony and year as random effects. Retained variables common to both systems are highlighted in gray. No predation metric was available for Common Tern models; all other variable groups were represented in both systems.

Prince William Sound - Kittiwakes **Gulf of Maine - Terns**

BINARY PRODUCTIVITY

Fixed effects

Coefficient	Estimate	SE	z	p
intercept	0.51	0.24	2.12	#
colony size	1.55	0.34	4.56	).001
wind	-0.52	0.18	-2.99	#
depth	-0.38	0.19	-2.03	#

Random effects

Intercept	Variance	SE
colony	0.717	0.847
year	0.341	0.584

POSITIVE PRODUCTIVITY

Fixed effects

Coefficient	Estimate	SE	t
intercept	0.51	0.02	22.92
predation	-0.17	0.01	-14.27
population density	0.08	0.02	3.89
rain	-0.02	0.01	-2.21
fish	0.03	0.01	2.45
colony size	-0.04	0.02	-2.08

Random effects

Intercept	Variance	SE
colony	0.011	0.104
year	0.000	0.000
residual	0.025	0.159

Fixed effects

Coefficient	Estimate	SE	t
intercept	0.98	0.04	27.85
population density	0.20	0.05	4.48
depth	-0.09	0.04	-2.27
colony size	-0.11	0.04	-2.61
wind	-0.07	0.03	-2.11
SST	0.07	0.03	2.20

Random effects

Intercept	Variance	SE
colony	0.000	0.000
year	0.003	0.052
residual	0.162	0.402

DISCUSSION

Food abundance vs. accessibility

Traditionally, we have perceived seabird populations largely to be regulated by prey availability (Ashmole 1963, Birkhead & Furness 1985), though there are exceptions (e.g., Frederiksen *et al.* 2008). When other elements affect breeding success, they often do so by altering food availability (e.g., Murphy *et al.* 1991, Wolf *et al.* 2009). We therefore expected to see dependency between prey and productivity in both kittiwakes and terns. While we did find an effect of herring spawning activity on kittiwake productivity, and both systems evidenced negative density dependence in productivity with respect to colony size, no tern prey metrics in the GOM provided sufficient explanatory power to our models to be retained in the selection process, and even in the PWS models, prey measures were not the strongest single-variable predictors.

Although we found no strong relationship between seabird productivity and our prey abundance indices, our results indicate that prey *accessibility* was important. Productivity in both systems was lower when summer winds were strong. Wind can affect seabirds in a number of ways. First, winds can directly impede flight; seabirds are known to avoid tailwinds in particular (Spear & Ainley 1997). Further, rough seas (generated by both local and distant winds) reduce feeding success (Pettingill 1939, Birkhead 1976), by either hampering foraging, obscuring prey from visual detection, or changing prey behavior (e.g., Finney *et al.* 1999). Wind can also affect prey indirectly via its influence on ocean production. Upwelling-favorable northeast winds in the GoM can increase the offshore transport of freshwater (Fong *et al.* 1997). Winds in PWS have more complex effects given its convoluted geography (Mooers & Wang 1998). Wind was

included in productivity models in both of our study systems; July N/S wind magnitude was an important predictor of binary kittiwake colony success in PWS, and June northeast winds were included in our top tern productivity model in the GOM. In both systems, the timing suggests that wind affects productivity via foraging efficiency more than via wind-driven ocean production.

Presumably, rain could also reduce prey accessibility by interfering both with flight and the ability to see food in the water; additionally, rain can directly reduce nestling survival by compromising young chicks' ability to thermoregulate (Schreiber 2002). Rainfall amount during the chick-rearing period is associated with poorer productivity in PWS kittiwakes; in contrast, we did not find a relationship between rain and tern productivity in the GOM. Extreme rain events are more likely in PWS, as it is a wetter system overall then the GOM. PWS qualifies as subpolar rainforest with an average annual precipitation of 760 to 4,060 mm compared to 1,050 to 1,250 mm in the GOM (McNab & Avers 1994). As cliff nesters, kittiwakes also are susceptible to nest failure during extended periods of heavy rain that can liquefy their mud-based nests and cause them to slip from the cliff face (pers. obs.).

Prey abundance may be a poor predictor of productivity for many reasons. Although lower trophic level species are the target of intensive fisheries activity in many regions, accounting for 30% of global marine capture fishery landings (FAO 2016), depletion of prey likely does not affect seabird productivity in the Gulf of Maine or Prince William Sound in most years. Atlantic herring in the GOM were not overfished as of 2011 (NEFSC 2012), and while PWS herring have yet to recover from a 1993 low (HRMT 2014), kittiwakes are generalist foragers (Dragoo *et al.* 2012), and other prey

(e.g., Pacific sand lance, capelin, salmonids) may be readily available. Further, productivity may be at least partially dependent on foraging success prior to the breeding season (Renner *et al.* 2014), a dynamic we were unable to capture in our analysis.

Intrinsic processes

Seabird productivity is relatively easy to quantify, making it a popular metric in efforts to use seabirds as indicators of marine systems (e.g., Cury et al. 2011), but intrinsic processes can potentially cloud the relationship between prey and seabird reproductive success. Cases of negative density dependence between colony size and reproductive success are well-documented (e.g., Hunt *et al.* 1986). This density dependence at least partially reflects a direct cost of large colony size via localized prey depletion (e.g., Lewis *et al.* 2001, Forero *et al.* 2002). To compensate, birds nesting in large colonies forage farther from the colony (Ainley *et al.* 2003, Grémillet *et al.* 2004). New, small colonies often are more productive than large, established colonies (e.g., Kildaw *et al.* 2005), possibly owing to a combination of greater prey availability (e.g., Tims *et al.* 2004), less familiarity to predators, and greater selection of non-degraded nesting habitat. Despite these benefits, birds exhibit some reluctance to form new colonies (Kildaw *et al.* 2005), suggesting there may be hidden costs associated with new colony formation.

Our results suggest that negative density dependence also may be driven by factors acting at colony sites. While we observed a negative effect of colony size on kittiwake and tern productivity, we observed a contrasting *positive* relationship between inter-colony competition (foraging area population density) and productivity in both

systems. While this relationship may simply indicate that successful colonies are located where the food is, it also hints that prey may not be the ultimate limiting factor on productivity in this system, a hypothesis further supported by the fact that food metrics were not supported in our analysis of tern productivity in the Gulf of Maine. Instead, we hypothesize that the negative effect of colony size likely reflected nest site limitation, as nest sites available to new recruits at large colonies may be marginal and poor in quality, driving the overall colony productivity down. Alternatively, negative density dependence could also be driven by increased predator attraction at large colonies.

Potential trade-offs between colony size and reproductive success merit further study, especially with regard to the effects of localized predation on productivity. While our top models of reproductive output, given success, in both systems included a negative relationship between colony size and productivity, our top reproductive success model in PWS showed the opposite relationship. Larger colonies were less likely to suffer complete reproductive failure; however, among colonies that produced chicks, larger colonies produced fewer chicks. We hypothesize that this pattern could indicate a predation effect. If food were the only limiting factor, we might expect large colonies to fail more often than small colonies owing to localized prey depletion, assuming a relatively even distribution of prey. Instead, we found small colonies were more likely to fail, a phenomenon that could result in part from localized predation activity and predator satiation (e.g., Patterson 1965) or more effective predation defense (e.g., Wiklund & Andersson 1994) in larger colonies. Alternatively, small colonies may exist in areas with less consistent prey resources.

Environmental factors and seabird productivity

DEPTH -- Both kittiwakes and terns are surface feeders, requiring prey to be close to the water's surface (*kittiwakes:* 1.0 m, Bayer 1983; *terns:* 0.5 m, Dunn 1972) for successful detection and capture. Surface foragers must either forage in shallow water or rely on other agents to aggregate prey within their reach, such as diving birds (e.g., Ostrand 1999), predatory fish (e.g., Hebshi *et al.* 2008) or marine mammals (e.g., Obst & Hunt 1990). Breeding kittiwakes in PWS generally forage in average ocean depths of 50 m (Maniscalco 1998); terns in the GOM are also nearshore foragers during the breeding season (Nisbet 1983). Given the propensity for birds of both species to forage nearshore (*kittiwakes:* Irons 1998; *terns:* Nisbet 2002), we expected foraging grounds that were shallower on average to correspond with greater productivity, as prey can use deep water as a refuge from aerial foragers. Instead, deeper foraging grounds were associated with greater productivity in both systems. This may reflect the tendency of complex bathymetry (combining shallow and deeper features) to enhance feeding opportunities (e.g., Schneider *et al.* 1990, Hunt *et al.* 1996)

SST - Links between SST and phenology are well-established for a number of species, where SST correlates with prey availability prior to the breeding season (e.g., Frederiksen *et al.* 2004b, Schultz *et al.* 2009). In kittiwakes, warm SST is associated with reduced prey availability early in the season, leading to later breeding (Shultz *et al.* 2009). Phenology can then affect reproductive success via timing mismatches between chick arrival and optimal chick meal availability (e.g., Watanuki *et al.* 2009, Burthe *et al.* 2012). In our analysis, we found a relationship between SST and productivity for terns

but not kittiwakes, despite the suggested link between SST and kittiwake phenology in other regions (Schultz *et al.* 2009, Moe *et al.* 2009). Our efforts were likely hampered by the low resolution of SST data available to match our time series. The fact that we did detect a link between SST and tern productivity in the Gulf of Maine, where warmer spring SST corresponded to greater productivity, may have been facilitated by the intensity of warming that occurred in the region during the period of our study (Pershing *et al.* 2015). We hypothesize that such a link might reflect a direct relationship between spring SST and later prey availability, as warm spring SST (Slater & Byrd 2009) and earlier breeding (e.g., Moe *et al.* 2009, McKnight *et al.* in prep.) can correspond with greater reproductive success.

CLIMATE -- Connections between seabird dynamics and large-scale climate patterns are well known. These can operate via phenology (e.g., Reed *et al.* 2006), particularly in long-range dispersers relying on large-scale cues to initiate their return to breeding grounds (e.g., NAO and kittiwakes/murres: Frederiksen *et al.* 2004b). Such distant cues may create timing mismatches that affect reproductive success (e.g., SST and kittiwakes: Hipfner 2008) and so are important considerations in any attempt to interpret seabird productivity patterns. Climate patterns can also alter a system's forage base by facilitating large-scale regime shifts (e.g., PDO: Anderson & Piatt 1999, Hatch 2012).

We found no apparent influence of any of the climate variables we included in our analysis. This is perhaps not surprising, given the relatively short time period of our study, especially for terns in the Gulf of Maine. Several of the indices we investigated were decadal or multi-decadal in period, so the majority of our data were collected during

a single phase. Further, we were most interested in exploring phenomena with direct influences on seabird dynamics (e.g., prey, weather); such factors would also serve as the pathways for indirect interaction between seabirds and large-scale climate patterns. In this case, we would expect the direct linkages to be supported more strongly in our modeling efforts.

Predation and brood size variability

Predation undoubtedly affects seabird reproductive success (e.g., Witham & Leonard 1999), but it is formidably difficult to quantify. Effects of predation vary widely among seabird colonies; nest predation is minimal on oceanic islands (e.g., Byrd et al. 2008) but can be substantial at coastal colonies accessible by mainland predators (e.g., Robbins 2009). Predation certainly affects seabird success in both PWS (Suryan *et al.* 2006) and the GOM (Nisbet & Welton 1984); however, we suspect that predation may play a greater role in shaping PWS productivity patterns, as all of the GOM colonies in this study experienced some level of predator control while PWS colonies did not. This discrepancy may explain the greater frequency of complete colony failures in PWS, where predation can be more important than food supply in regulating seabird populations (Bixler *et al.* 2010).

Brood sizes at fledging are typically larger for PWS kittiwakes than for kittiwakes nesting in the Pribilofs, despite similar initial clutch sizes (Irons, unpublished data). The difference suggests that food may be more limiting for Pribilof kittiwakes; chick starvation likely triggers siblicide across colonies, so that fledging brood sizes greater than one are quite rare (Irons, unpublished data). In contrast, two chick nests were fairly

common in PWS, even in years of relatively poor productivity, leading to greater variability in brood sizes at fledging within colonies. We suspect that predation caused much of the observed nestling mortality and that variability in fledging brood sizes over plots within a colony was a reasonable proxy for predation pressure. We presume that prey limitation would have a more uniform effect over plots than predation, given the sequential way that predators work through kittiwake colonies (US FWS, unpublished data).

One possible drawback of using variation in fledging brood size as a predation index is the potential contribution of heterogeneity in adult quality among plots. Coulson (1968) found that higher quality kittiwakes at his warehouse colony nested in center plots where they enjoyed greater reproductive success than edge nesters. Such varying parental quality over plots could confound our metric, as the brood size difference between high and low quality parents may be more distinct in years of poor prey availability. In natural colonies with truly heterogeneous nesting habitat, however, more complex dynamics are likely at play (Velando & Freire 2001, Descamps *et al.* 2009); nesting habitat quality may vary at relatively small scales within larger nesting patches. Plots in PWS are fairly large and contain diverse nesting habitat (Robbins 2009). Further, no nest is truly safe from predators; although mammalian and large avian predators may be restricted to wide, gently sloping ledges, they are often accompanied by opportunistic caching predators (e.g., Northwestern Crows [Corvus caurinus] or Black-billed Magpies [Pica hudsonia]) with no such restrictions. These satellite predators take advantage of large sections of the colony being flushed off their nests by more formidable predators (Robbins 2009). Fledging brood size variability was the best single variable predictor of kittiwake

productivity and its inclusion in the top multivariable models of kittiwake productivity support the hypothesis that predation strongly influences kittiwake productivity in PWS.

MANAGEMENT IMPLICATIONS

Human activity substantially affects the majority of marine ecosystems across the globe (Halpern *et al.* 2008). In response, natural resource conservation and management strategies are shifting from species-specific approaches to ecosystem-based approaches and marine spatial planning (e.g. United Nations Educational, Scientific, and Cultural Organization Marine Spatial Planning Initiative, Executive Order No. 13547, Magnuson-Stevens Reauthorization Act 16.US.C. § 1801(3)(3), NOAA Next-Generation Science Plan, U.S. Fish and Wildlife Service National Wildlife Refuge System), yet the relationships among organisms, and between organisms and their physical environment are not always well understood (Weimerskirch et al. 2003; Arkema et al. 2006; Leslie & McLeod 2007). Our limited understanding of complex ecological interactions hinders our assessment of biological dynamics of marine ecosystems and potential effects of large-scale environmental disturbances such as climate change (Griffies 2004). While we have long understood the direct relationship between prey abundance and seabird reproduction, here we identify weather-related factors that may mediate this relationship via direct effects on foraging efficiency and nestling survival. Increasing frequency and intensity of weather events associated with climate change (IPCC 2014) may therefore have stronger effects on seabird populations than anticipated. Our work highlights the need for continued monitoring of seabird populations coupled with directed

investigations that can quantify the links between mediating environmental influences and seabird population dynamics.

ACKNOWLEDGEMENTS

Gulf of Maine tern data were supplied by the Gulf of Maine Seabird Working Group. Sally Sherman of the Maine Department of Marine Resources supplied fish data from the Maine-New Hampshire inshore trawl survey. Steve Moffitt of the Alaska Department of Fish & Game (ADF&G) provided pink salmon run data; ADF&G is not responsible for errors or deficiencies in reproduction, subsequent analysis, or interpretation of salmon data. Grant Humphries of Black Bawks Data Science provided valuable assistance in wind data summary. Reviews by Jeffrey Runge, Erik Blomberg, and Brian Olsen greatly improved this manuscript. Funding for the PWS fieldwork was provided by the U.S. Fish and Wildlife Service, and the *Exxon Valdez* Oil Spill (EVOS) Trustee Council. Administrative, financial, and computer support during data analysis and manuscript development was provided by the University of Maine through the Cooperative Agreement with the U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit. This study does not necessarily reflect the views of the EVOS Trustee Council or the U.S. Fish and Wildlife Service. Mention of trade names and commercial products does not constitute endorsement or recommendation for use by the U.S. Government.

CHAPTER 3: INFLUENCE OF AGE AND MULTIPLE STRESSORS IN SHAPING SEABIRD PRODUCTIVITY

ABSTRACT

While we have a good understanding in many systems of the effects of single variable changes, we understand far less about how variables act in concert, where interactions can lead to unanticipated results. We evaluated effects of multiple variables that we expected to play a role in the early reproductive stages of a North Pacific seabird from 1992 – 2008. Our work revealed the potential for contrasting stressor effects across successive stages of reproduction. Bird age, timing of egg laying, and winter ENSO conditions best explained individual laying success, such that laying success was lower when birds were younger, the average winter ENSO index was negative (as occurs during El Niño episodes), and median laying date for the colony was later. Age and salmon run timing (a proxy for predator presence at the colony) best explained hatching success, such hatching success was poorer when birds were young and when salmon runs were late. Identifying such differential effects of multiple stressors across consecutive reproductive stages can greatly enhance our ability to interpret trends and manage populations in the face of anthropogenic changes currently occurring in living systems.

INTRODUCTION

The ecological literature is replete with experiments documenting the effects of biotic and abiotic factors acting singly on a vast assortment of ecological levels, taxa, and morphological, physiological, and genetic expressions of individual organisms. We increasingly recognize, however, that in nature, organisms, populations, and communities

do not experience such influential forces in a vacuum; instead, multiple stressors (i.e., factors that can cause adverse effects) act simultaneously on a system, interacting additively, antagonistically (i.e., combined effects are less severe than the sum of individual effects), or synergistically (i.e., combined effects are more severe than the sum of individual effects; Folt et al. 1999, but see Piggott et al. 2015) to affect the system in complex ways. These interactions can be further complicated by the pathway of each stressor's effect; some may affect an organism directly, while others may act indirectly by altering the effects of another stressor (Ban et al. 2014). Stressors that have little influence on their own can have substantial effects in combination (e.g., Gentes et al. 2006, Hallinger & Cristol 2011), and non-additive interactions may lead to unexpected outcomes (e.g., Ormerod et al. 2010, Jackson et al. 2016). Several reviews of controlled experiments across a wide range of taxa and environments suggest that interacting stressors often do have non-additive effects (e.g., Darling & Cote 2008), especially in marine systems (e.g., Crain et al. 2008).

As part-time denizens of two systems (marine and terrestrial), breeding seabirds provide us with an ideal case study for investigating how multiple factors may act in concert to influence population vital rates. All seabirds are tied to terrestrial nesting sites during the breeding season but must acquire food for themselves and their offspring from the marine environment. Seabirds are currently undergoing dramatic global declines (Paleczny et al. 2015); their downward population trends combined with their potential role as marine indicators (e.g., Einoder 2009, Le Bohec et al. 2013) provide powerful incentives for us to understand how environmental and biological factors from both systems combine to affect seabird population parameters.

Seabird species are generally long-lived; evidence suggests that adult survival is well-buffered against environmental perturbation (e.g., McKnight et al. *in prep* (COR paper!), Schmidt et al. 2015). In contrast, seabird reproductive parameters (e.g., hatching success, provisioning trip duration, fledgling mass) are more sensitive; stressor effects are likely more detectable in breeding metrics than in other aspects of seabird biology. Many studies have focused on the effects of food supply on seabird reproductive success (i.e., fledgling production per breeding attempt; e.g., Cury et al. 2011), a widely used (e.g., Dragoo et al. 2012) and relatively cost-effective metric that can be estimated from one or two visits to a breeding colony. However, seabird reproductive success is a multi-step process involving a sequence of events from nest site establishment and mate acquisition through egg production and incubation, culminating in successful chick rearing. Reproductive success therefore integrates the effects of a variety of factors that differentially affect each stage of the process (Etterson *et al.* 2011) and may therefore be largely buffered by competing forces at different stages, obscuring relationships between stressors and seabird breeding parameters.

At the colony level, events affecting early stages of reproduction could be masked by later events with opposing effects on reproductive success. For example, negative effects associated with high breeder mortality prior to the breeding season can be partially compensated by increased recruitment of pre-breeders (e.g., Porter & Coulson 1987). Likewise, when populations exist under density-dependent controls (e.g., Lewis *et al.* 2001), heavy mortality of eggs or young nestlings may release survivors from the effects of prey limitation. Such confounding effects may hinder our attempts to understand and interpret patterns in seabird reproductive success.

Although many studies have investigated reproductive success at the level of a colony or regional population (e.g., Dragoo *et al.* 2012), comparatively few have done so at the level of individual breeders, which is necessary to identify contrasts in stressor effects among reproductive stages. Further, individual characteristics (e.g., physical condition, age, phenotype) can lead to correlation in the probabilities of success across reproductive stages and breeding attempts in long-lived seabirds. In particular, reproductive success can vary with age, where success is relatively poor in young birds (e.g., Wooller et al. 1990, Weimerskirch 1992) and gradually improves with age (e.g., Ollason & Dunnet 1978, Sydeman *et al.* 1991, Green 2001). Inherent quality (i.e., individual variation in performance that persists over a lifetime) can affect both survival and reproductive success, where better quality individuals may secure more resources seemingly without incurring extra costs (e.g., Cam *et al.* 2002), allowing them to both survive and reproduce better than lesser quality counterparts (van Noordwijk & deJong 1986).

How do multiple stressors combined to affect sequential breeding stages in individual seabirds? While we know that food quality and availability are crucial during the chick rearing period (e.g., Jodice et al. 2006), other biological and environmental conditions prior to hatching also may be important to seabird productivity. Our objective was to evaluate contributions of multiple environmental, biological, and individual variables and their interactions at multiple reproductive stages, including laying (Table 3.1) and incubation (Table 3.2) in a long-lived colonial seabird. We tested hypotheses describing laying success as a function of breeder age, winter conditions, spring conditions, early breeding season conditions, population size, carryover effects, and

combinations of the above. We also tested hypotheses describing hatching success as a function of these same factors as well as incubation weather and predation.

METHODS

Focal species

The Black-legged Kittiwake (*Rissa tridactyla;* "kittiwake" hereafter) is a small, long-lived (mean life expectancy at a North Pacific colony = 13 years; Hatch, Roberts & Fadely 1993) gull with a circumpolar distribution throughout the northern hemisphere and a global population size estimated to be from 17 to 18 million individuals (Delany & Scott 2006). They are largely piscivorous, foraging in both nearshore and pelagic habitats. Many questions remain about their winter distribution; kittiwakes from Prince William Sound can disperse widely throughout the North Pacific during the non-breeding season but may not always do so (McKnight et al. 2011), a behavior that may depend upon the severity of weather in the northern Gulf of Alaska. Kittiwakes are colonial cliff-nesters, rearing one, two, or rarely three young per breeding season. As in many seabird species, both parents share incubation and chick-rearing duties equally (Coulson & Wooller 1984). Both mate- and nest-site fidelity are high (Coulson & Thomas 1985).

Site description

The Shoup Bay kittiwake colony is located in northeastern Prince William Sound (PWS), Alaska (61° 10' N, 146° 35' W; Fig. 3.1). Shoup Bay is a fjord that adjoins Port Valdez with a tidewater glacier that terminates at the fjord's western end. The fjord connects to Prince William Sound via a reversing tidal river 0.7 km in total length.

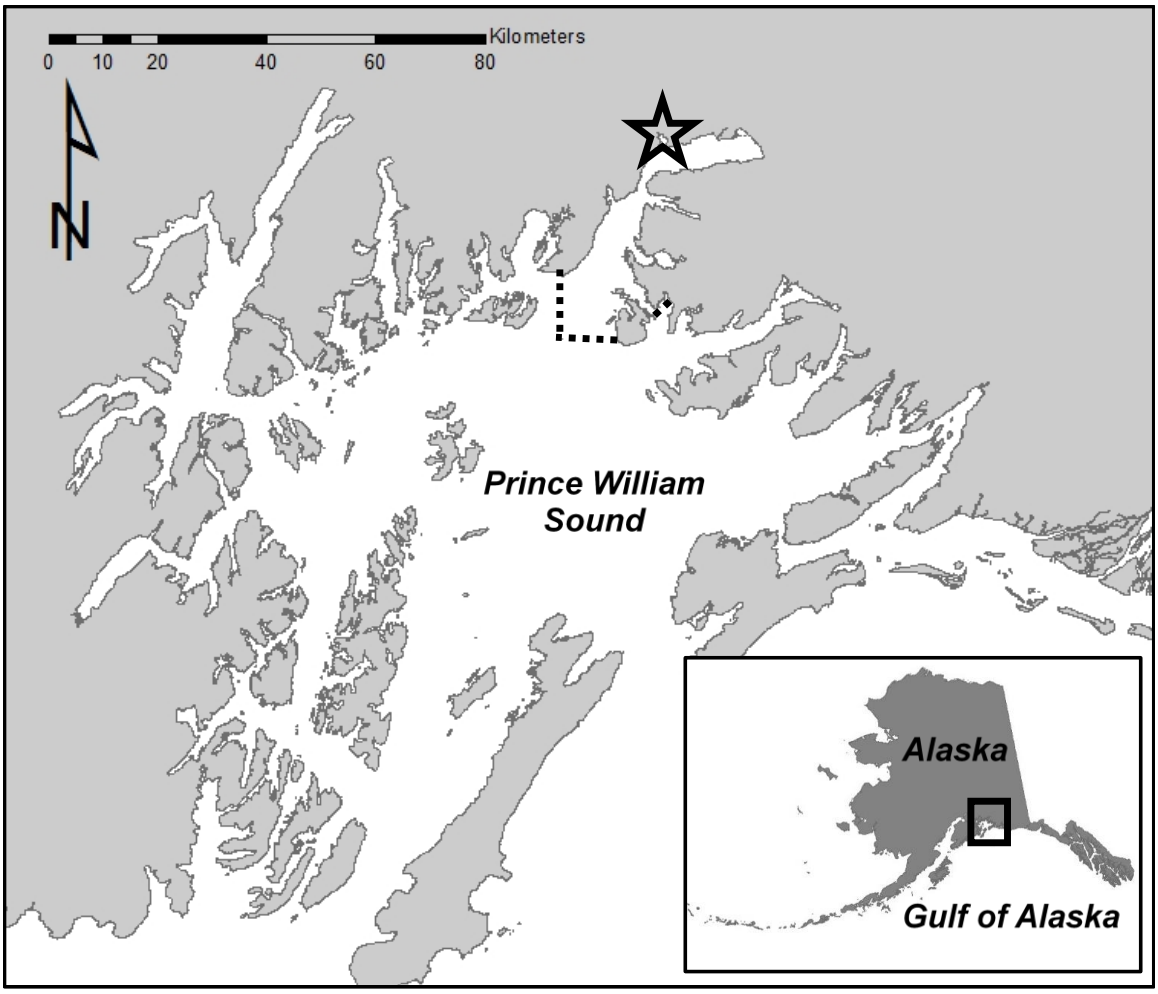

Figure 3.1. Study site. Location (star) of the Shoup Bay kittiwake colony in Prince William Sound, Alaska. Dotted line represents the approximate boundaries of fisheries subdistricts providing salmon timing data. Inset map shows the location of Prince William Sound within Alaska.

Through the early 2000s, the fjord was frequently filled with large icebergs calved from the glacial face. By the late 2000s, the glacier had retreated mostly onto land and the fjord became mostly iceberg-free. The kittiwake colony is located primarily on the south-facing side of a rocky island ~0.4 km in length and ~100 meters from the mainland. Based on annual nest counts starting in 1985, colony size peaked in 2002 with 19,000 actively breeding birds but declined to 14,100 active breeders by 2008, the final year of

Table 3.1. Single variable hypotheses for laying success. Single variable hypotheses to explain laying success in known-aged Black-legged Kittiwakes from the Shoup Bay colony in Prince William Sound, Alaska, U.S.A., along with variables and their sources used in generalized linear mixed models to represent each hypothesis. "Winter" refers to monthly data from November through February prior to the breeding season; "spring" refers to monthly data from March through April prior to the breeding season.

Hypothesis	Variables	Source
Laying success is a function of age.		
	Individual kittiwake age	US FWS Monitoring data
Laying success is a function of winter conditions.		
	Mean winter PDO index values	JISAO 2016
	Mean winter Nino 3.4 index values	ESRL 2016a
	Mean monthly modeled winter winds in northern GOA	ESRL 2016b
	N/S vector component	
	Absolute value N/S vector component	
	E/W vector component	
	Absolute value E/S vector component	
	Absolute value combined vectors	
	Mean monthly winter sea surface temperature	ESRL 2016c
	Prince William Sound (60N, 147W)	
	Northern Gulf of Alaska (58N, 147W)	
	Maximum monthly winter sea surface temperature	ESRL 2016c
	Prince William Sound (60N, 147W)	
	Northern Gulf of Alaska (58N, 147W)	
Laying success is a function of pre-breeding conditions.		
	Median laying date	US FWS Monitoring data
	Mean monthly modeled spring winds in northern GOA	ESRL 2016b
	N/S vector component	
	Absolute value N/S vector component	
	E/W vector component	
	Absolute value E/S vector component	
	Absolute value combined vectors	
	Mean monthly spring sea surface temperature	ESRL 2016c
	Prince William Sound (60N, 147W)	
	Northern Gulf of Alaska (58N, 147W)	
Laying success is a function of early breeding conditions.		
	Mean incubation body condition	US FWS Monitoring data
Laying success is a function of population size.		
	Number of nesting pairs at the Shoup colony	US FWS Monitoring data
Laying success is a function of carryover effects from previous season.		
	Colony productivity in previous season	US FWS Monitoring data

this study. Predators at the colony are predominantly avian and include Bald Eagles *(Haliaeetus leucocephalus),* Peregrine Falcons *(Falco peregrinus),* Common Ravens *(Corvus corax),* Northwestern Crows *(Corvus caurinus),* and Black-billed Magpies *(Pica hudsonia).* Occasional mammalian predators include American mink *(Neovison vison)* and wolverine *(Gulo gulo).*

Field data collection

LAYING/HATCHING SUCCESS OF KNOWN-AGED INDIVIDUALS -- Annually during 1979 and 1988-2008, we banded up to 600 (369 ± 74; reported ranges denote 95% confidence intervals) 12-32 day-old kittiwake chicks at the Shoup colony. We individually marked chicks with either a three-band cohort-specific mark or a unique color band combination. Four to eight observers resighted (with binoculars and 60X spotting scopes) color-banded birds during 1992 – 2010 in mornings and evenings in May when breeders were actively building nests. We divided the colony into ten major nesting section, delineated by easily discerned cliff features, and sections were resighted 9.8 ± 0.7 times on average each year between 1998 and 2010 (the period of time when section-specific effort records are available); resighting effort in earlier years was comparable. We evaluated each individual's breeding status based on the number of times it was recorded at a particular nest site, as holding a nest site is the essential condition that affects kittiwake survival irrespective of reproductive success (Aubry et al. 2011) and is thus a good indicator of an individual's intent to breed. Birds seen at a particular nest site three or more times were considered to be probable breeders ("breeders" hereafter). Birds seen fewer than three times on a single site were noted as

Table 3.2. Single variable hypotheses for hatching success. Single variable hypotheses to explain hatching success in known-aged Black-legged Kittiwakes from the Shoup Bay colony in Prince William Sound, Alaska, U.S.A., along with variables and their sources used in generalized linear mixed models to represent each hypothesis. "Winter" refers to monthly data from November through February prior to the breeding season; "spring" refers to monthly data from March through April prior to the breeding season.

Hypothesis	Variables	Source
Hatching success is a function of age.		
	Individual kittiwake age	US FWS Monitoring data
Hatching success is a function of winter conditions.		
	Mean winter PDO index values	JISAO 2016
	Mean winter Nino 3.4 index values	ESRL 2016a
	Mean monthly modeled winter winds in northern GOA	ESRL 2016b
	N/S vector component	
	Absolute value N/S vector component	
	E/W vector component	
	Absolute value E/S vector component	
	Absolute value combined vectors	
	Mean monthly winter sea surface temperature	ESRL 2016c
	Prince William Sound (60N, 147W)	
	Northern Gulf of Alaska (58N, 147W)	
	Maximum monthly winter sea surface temperature	ESRL 2016c
	Prince William Sound (60N, 147W)	
	Northern Gulf of Alaska (58N, 147W)	
Hatching success is a function of pre-breeding conditions.		
	Median laying date	US FWS Monitoring data
	Mean monthly modeled spring winds in northern GOA	ESRL 2016b
	N/S vector component	
	Absolute value N/S vector component	
	E/W vector component	
	Absolute value E/S vector component	
	Absolute value combined vectors	
	Mean monthly spring sea surface temperature	ESRL 2016c
	Prince William Sound (60N, 147W)	
	Northern Gulf of Alaska (58N, 147W)	
Hatching success is a function of incubation conditions.		
	Mean incubation body condition	US FWS Monitoring data
	Precipitation	NCEI 2016
	Number of days in June with precipitation >2.54mm	
	Mean daily maximum precipitation in June	
	Mean precipitation in June	
	Temperature	NCEI 2016
	Mean daily maximum temperature in June	
	Mean temperature in June	
Hatching success is a function of eagle predation.		
	Salmon run timing (alternate eagle prey)	ADFG 2014
	Julian date when salmon landings surpass 30,000 fish	
	Julian date when salmon landings surpass one million fish	
	Salmon run magnitude	ADFG 2014
	Total salmon landings for the season	
Hatching success is a function of population size.		
	Number of nesting pairs at the Shoup colony	US FWS Monitoring data
Hatching success is a function of carryover effects from previous season.		
	Colony productivity in previous season	US FWS Monitoring data

probable non-breeders ("non-breeders" hereafter), i.e., they were present but not engaged in intensive nesting behavior. While predation was substantial during some years (and was the proximate cause of nearly all of nest failures), the majority of predation occurred following the period when we resighted marked individuals at the colony, and thus did not appreciably influence breeding status assignments by removing banded breeders prior to their third sighting.

Each year, we monitored contents of accessible nests (N = 120 ± 40) belonging to known-aged breeders every three days from the beginning of the incubation period until the research crew departed in early August. To improve sample sizes of older (>16 years) birds, we included individuals banded as adults (minimum age = 2 years) in 1991 in the 2006-2008 samples. While the bulk of nests had either failed or fledged chicks by the time we ceased monitoring each year, we were often unable to document the final fate of late-hatching chicks; we therefore restricted our investigation to laying success (i.e., whether one or more eggs were laid in the nest of a probable breeder) and hatching success (i.e., whether one or more eggs hatched in probable breeders' nests where one or more eggs were laid).

MEDIAN LAYING DATE -- We also collected annual nest survival data for nests located in ~15 permanent "productivity plots" that included both edge and central nesting habitat patches. We took Polaroid photos of each productivity plot section as seen from above and numbered all the nests (N~30 per photo) visible from the photo vantage point. We recorded the contents of each nest every three days beginning prior to egg laying. Because we were interested only in calculating a median lay date from these data, we

combined plots into a simple random sample representing the entire colony. We used these data to calculate the median date that the first egg was laid in each nest, and used this metric to represent breeding season phenology, which reflects local forage conditions immediately prior to the kittiwake breeding season in Alaska (Moe et al. 2009, Shultz et al. 2009), as seabirds likely must attain a minimal body condition threshold before commencing breeding (e.g. Sorenson *et al.* 2008). We also calculated the median date that the first chick hatched in each nest as an alternative phenology metric, though hatch timing potentially could be uncoupled from breeding commencement if clutches are replaced or the onset of incubation is delayed.

ADULT BODY CONDITION -- We randomly selected and captured adult kittiwakes during different stages of the breeding season each year during 1995 and 2008 for body condition assessment. Capture devices included snare traps set on the nest or roosting rock, telescoping noose poles, and dipnets, and trapping locations were chosen from regions of the colony cliffs accessible from above or below by scrambling, by boat, or by extension ladder. We recorded the nest contents of each bird, then measured its mass, head-bill length (head), diagonal right tarsus length (tarsus), and flattened right wing length (wing). We noted any existing leg band combinations and banded any previously unmarked birds with unique color band combinations.

BREEDING POPULATION SIZE AND PRODUCTIVITY -- Beginning in 1985 and continuing to the present, we visited the Shoup Bay kittiwake colony in PWS annually as part of a larger effort to document breeding effort and productivity at all kittiwake

colonies in Prince William Sound. In late May/early June, when birds had begun incubation, we counted all active nests (attended by at least one bird) on all faces of the colony with binoculars from a boat. We then counted all chicks present at the end of the chick-rearing period (late July/early August) and divided the total number of chicks by the total number of nests each year to calculate colony productivity.

Data analysis

BODY CONDITION INDEX -- We used average body condition to represent forage conditions during the laying and incubation stages. To this end, we developed a body condition index for all adults measured from 1996 - 2008 (N = 1154 observations) using the percent difference between predicted and observed mass as predicted by structural body size. We created the body size index from the first principal component (PC) of a principal components analysis (PCA) of the body size measurements for all bird observations with complete measurements (head, tarsus, and wing; N=1034) conducted using the *prcomp* function from the stats library in Program R (R Core Team 2016). Next, we calculated the body size index value for all birds and regressed mass on body size index value using the *lm* function (R Core Team 2016).We then interpolated missing tarsus measurements from 1996 and 2000 (N = 49) using a linear regression of tarsus predicted by head and wing size for all birds and calculated their body size index values using interpolated tarsus values. Finally, we used the percent difference between predicted and observed masses as the bird's body condition index value, with positive body condition index values indicating that a bird had more mass than predicted based on its size ("good" condition) (Table 3.3). We averaged within-year body condition index

Table 3.3. Body condition equations. Equations developed to describe body condition using principal components analysis of size metrics regressed on mass for Black-legged Kittiwakes captured at the Shoup Bay colony in PWS, AK between 1996 and 2008.

Equation	**Formula**
Structural size PC1	$PC1 = -0.613 \times head - 0.553 \times tarsus - 0.564 \times wing$
Tarsus prediction	$tarsus = 0.188 \times head + 0.025 \times wing + 9.641$
Mass prediction	$\ln(mass) = -0.098 \times \ln(body\ size\ index + 3.6) - 6.14$
Body condition index	$body\ condition\ index\ value = 100 * \frac{(observed\ mass - predicted\ mass)}{predicted\ mass}$

values for all birds measured during the incubation period (May) each year, thus generating a single average incubation body condition value per year to use in reproductive success modeling. Because the average body condition variable was only available for 1996 on, we restricted our analysis to laying and hatching success between 1996 and 2008. Sex was unknown for most birds; however, while size is known to differ by sex in kittiwakes (Jodice *et al.* 2000), Golet and Irons (1999) found that the relationship between body size and mass was not significantly different between males and females.

REPRODUCTIVE EFFECTS MODELING -- In addition to breeding kittiwake metrics described above, we also modeled reproductive success as a function of a number of

environmental factors we hypothesized might affect kittiwake survival and recruitment (Tables 3.1 and 3.2). First, we calculated the mean winter (November through February) Pacific Decadal Oscillation index value prior to the breeding season using index values representing the first principal component of North Pacific (> 20° north latitude) monthly sea surface temperature anomalies (JISAO 2016). We computed a similar mean winter El Niño – Southern Oscillation (ENSO) index value from a five month running mean sea surface temperature anomaly in the region between 5°N-5°S and 170°W- 120°W (ESRL 2016a). We suspected that migratory decisions might be made based on local conditions affecting forage efficiency, specifically wind and sea surface temperature. For an index of winter and spring (March through April) weather conditions in the northern coastal shelf of the Gulf of Alaska, we extracted and averaged mean monthly modeled wind magnitudes for 59°N 147°W *(*ESRL 2016b). We similarly averaged monthly optimally interpolated sea surface temperatures (ESRL 2016c) for two representative locations that might be used by non-migrating individuals in the winter (McKnight *et al.* 2011): Prince William Sound (60°N, 147°W) and the northern coastal shelf of the Gulf of Alaska (59°N, 147°W) for both winter and April, the month prior to commencement of breeding activity. To characterize temperature and precipitation patterns experienced during incubation each year, we acquired June temperature and precipitation metrics documented by the Valdez Weather Service Office (61.13°N, 146.35°W), including mean temperature, mean maximum daily temperature, mean daily precipitation, mean maximum daily precipitation, and the number of June days with precipitation > 2.54mm (NCEI 2016). To characterize predation, we obtained pink salmon harvest data for Valdez Arm and Port Valdez from Steve Moffitt of the Alaska Department of Fish and

Game (ADFG 2014). From these, we calculated two phenology metrics (calendar dates, adjusted for leap years, when the annual harvest surpassed 30,000 and one million fish, respectively) to represent the duration of pre-salmon run eagle attendance at the colony, along with the total seasonal harvest. We centered and scaled all continuous covariates prior to modeling.

We used the *glmer* function from the lme4 library (Bates et al. 2014) in Program R (R Core Team 2016) to build mixed effects models investigating relationships between laying and hatching success of individually identifiable birds and age, colony size, phenological timing, condition, previous productivity, winter and spring winds, winter and April SST, and climate. We designated individual bird identity and nested colony section (southern islands, south end, central face, north end, and back side) within year as random effects to account for changes in section quality over time as the colony expanded and contracted. We modeled the probability of success as a binomial variable with a logit link and used the bobyqa optimizer as the numerical optimization algorithm. During each analysis set we evaluated the top model's residual distribution, normality, and dispersion to assess whether model assumptions were met. If residuals were sufficiently homoscedastic and were either normally distributed, or if not, then at least not overdispersed, we accepted the model fit as sufficient.

Prior to multi-variable modeling, we identified the best representative metric within each group (e.g., winter wind metrics) by building and comparing single variable models using AIC model selection. Top-ranked variables within each group that outperformed the null model and were not correlated ($r \geq 0.65$) with a higher ranked representative variable were used in subsequent modeling. We combined these best-

performing metrics to build a global model, then tested for the ability of each variable to improve the model by comparing model performance, via AIC score, of the global model versus the model with each individual variable removed ("global minus one" model sets). Variables whose omission worsened the AIC score by more than two AIC units were included in the final model. For variables whose omission worsened the global model's AIC score by fewer than two AIC units, we assessed their relative contribution by (1) performing an analysis of variance (ANOVA) between the global model and the model missing the variable in question and (2) building and comparing AIC values for additive models of key variables both including and excluding the variables in question ("key variable" model sets). If more than one key variable model was competitive (i.e., within 2 AIC units of the top-scoring model), we evaluated support for retaining the additional variable via an ANOVA comparison.

Model validation

Although our primary purpose was hypothesis testing, we also tested the predictive power of top models by using them to predict success for observations of birds were not individually identifiable and thus not used in the training dataset, substituting zero for the random effect coefficient associated with individual identity for each record. We iteratively determined the probability threshold value (to the nearest 0.01) that optimized the proportions of both correctly predicted successes and failures.

RESULTS

Body condition index

We captured 86 ± 26 (mean ± 95% CI) randomly selected birds each year for body condition assessment. Of these, 41 ± 10 were captured each June while incubating eggs. Because the first PC of the PCA explained 64% of the variance in the data, we felt it was sufficient to use alone in calculating a body size index for each individual. The linear regression of tarsus predicted by head and wing measurements produced homoscedastic, normally distributed residuals and an R^2 value of 0.26. The regression of the natural logarithm of mass on the natural logarithm of body size produced homoscedastic, normally distributed residuals and an R^2 value of 0.25 (Table 3.3).

Laying success

MODEL RESULTS -- We modeled laying success using 1,596 observations of 878 known-aged individuals from 1996 – 2004 and 2006 – 2008, representing 1,246 successes and 350 failures. Forty-two percent (N=372) of the individuals were observed in more than one year. The top-ranked single-variable model explaining laying success included only age as a fixed effect (Aikake weight $w_i > 0.99$; Table B1). Median first lay date was the second-best predictor of laying success ($\Delta AIC = 47.57$). While AIC selection favored the retention of colony size in the final model multivariable model, ANOVA results favored its elimination ($p = 0.06$) and the reduced model performed equivalently during validation. Our final multivariable model of laying success therefore included only additive effects of age, median first lay date, and winter ENSO index ($w_i = 0.32$; Tables B2 & B3), such that laying success was lower when the average winter

ENSO index was negative (as occurs during El Niño episodes) and median laying date for the colony was later. This model far outperformed the "age only" model (ΔAIC = 45.72) and was competitive with the top-scoring "global minus one" model ("global – spring wind"; ΔAIC = -1.28).

VALIDATION -- The laying success validation dataset included 617 records; of these, 537 represented successes and 80 represented failures. Prediction using the final model was best using a cutoff of 0.86 (predicted laying success of 0.86 or higher = "success," less than 0.86 = "failure). Using this cutoff value, 64% of successes, 65% of failures, and 64% of overall outcomes were correctly predicted by the top model. Including colony size in the model did not substantially change its predictive ability; prediction in this case was best using a cutoff value of 0.85, with 65% of successes, 63% of failures, and 64% overall outcomes correctly predicted.

Hatching success

MODEL RESULTS -- We modeled hatching success using 1,246 observations 733 known-aged individuals from 1996 – 2004 and 2006 – 2008, representing 562 successes and 684 failures. The top-ranked single-variable model explaining hatching success included only salmon timing (w_i = 0.27; Table B4). Colony size was the second-best predictor of hatching success (ΔAIC = 0.61, w_i = 0.20). Multivariable modeling identified only age and salmon timing as influential when all variables were considered simultaneously ("global minus one" model ΔAIC = 2.92 and 4.28, respectively). The final multiple-variable model of hatching success included additive effects of age and the

calendar date when the pink salmon harvest exceeded 30,000 fish (w_i = 0.14 when included with all "global minus one" models; Tables B5 & B6), such hatching success is poorer when birds are young and when salmon runs are late.

VALIDATION -- We applied top hatching success model coefficients (both fixed and random) to the data held out of the original hatching success modeling effort. This validation dataset included 537 observations of non-individually identifiable birds; of these, 279 represented successes and 258 represented failures. Prediction was best using a cutoff of 0.52 (predicted laying success of 0.52 or higher = "success," less than 0.52 = "failure). Using this cutoff value, 75% of successes, 73% of failures, and 74% of overall outcomes were correctly predicted by the final model.

DISCUSSION

Patterns in laying and hatching success

Renner et al. (2014) and Schultz et al. (2009) found a strong relationship between phenology and population-level laying success in kittiwakes breeding in the Bering Sea and the northern Gulf of Alaska, respectively. The Gulf of Alaska study, along with a similar study in the high Arctic north of Norway further revealed that phenology was coupled with SST (Moe et al. 2009, Schultz et al. 2009) and corresponding patterns of fish availability, where years with colder SST had higher fish availability, allowing for earlier egg laying in kittiwakes (Schultz et al. 2009). While we found a similar link between phenology and laying success in Shoup kittiwakes, we found no comparable relationship between spring SST and laying success in our work, which may reflect our

use of a coarser SST metric or, alternatively, a different prey/oceanography dynamic in PWS kittiwakes. The fact that phenology had such a strong relationship with laying success in three Alaskan populations with very different diet compositions (Dragoo et al. 2012) suggests that phenology drives laying success via some overarching process (e.g., spring bloom) that transcends specific diet composition.

Population-level hatching success in kittiwakes from the Pribilof Islands in the Bering Sea, more than 300 km from the mainland and its predator populations, was associated with both laying success as well as the previous year's colony-wide reproductive success (Renner et al. 2014). In contrast, we found no relationship with the previous year's colony success, which suggests that other factors, such as predation, may dampen any corresponding temporal correlation in annual productivity for Shoup Bay kittiwakes. Instead, age and salmon run timing had the strongest relationship with hatching success in Shoup Bay kittiwakes of the variables we investigated.

Many studies have shown a trend toward greater reproductive success with age in seabird populations. This phenomenon in part reflects selective elimination of poorer quality individuals (Cam *et al.* 2002, Aubry *et al.* 2009, Lescroel *et al.* 2009), which can cause an apparent increase in quality of a cohort through time (Cam & Monnat 2000). Learning, including greater foraging experience in the marine environment, also contributes to greater breeding success in older birds (e.g., Porter & Sealy 1982, Fayet *et al.* 2015). Our results reflect this age trend; we found that both laying success and hatching success in Shoup kittiwakes increased with age. The age effect was most apparent in our laying success modeling, where age was by far the best single predictor of success. Age was a less influential predictor of hatching success, likely owing in part to

the conditional nature of our analysis, as unsuccessful layers were not included in hatch success modeling.

While predation is generally acknowledged to affect seabird reproductive success (e.g., Witham & Leonard 1999), it is difficult and labor-intensive to quantify. Effects of predation vary among kittiwake colonies; nest predation is minimal in the oceanic Pribilof Islands (Byrd et al. 2008), but it can be substantial at coastal colonies accessible by mainland predators. Robbins (2009) found that Bald Eagles in particular posed a triple threat to Shoup kittiwakes; not only did they take an occasional adult, but their presence at the colony while hunting kept kittiwakes off their nests, exposing eggs to opportunistic scavengers and the elements. According to our top models, hatching success at the Shoup colony is lower in years with later salmon runs; we attribute this pattern to prolonged eagle presence at the colony when salmon runs are late. Because predation may vary annually, as in this case, identifying a proxy metric for predation effects can improve predictions of seabird productivity; including salmon timing in our analysis resulted in an improvement of $\Delta AIC = 9.07$ over the model with age alone.

Multiple stressors

Laboratory work on smaller organisms shows that in contrast to freshwater systems, where the majority of stressor interactions are antagonistic (Jackson et al. 2016), marine populations are more apt to experience synergistic interactions (Crain et al. 2008). Testing for such interactions in highly mobile macrofauna is somewhat more challenging, however, as it is virtually impossible to establish controlled experimental conditions in the field. Despite this limitation, researchers have identified synergistic interactions

between food shortage and predation on seabird reproductive success (Regehr & Montevecchi 1997) by modeling data collected in the field. Our work revealed the potential for contrasting stressor effects across successive stages of reproduction. For example, the positive influence of an early salmon run on hatching success may partially compensate for negative effects of winter ENSO conditions on laying success. Likewise, poor winter ENSO conditions coupled with a late salmon run could pack a sequential double whammy on laying and hatching success. Identifying such differential effects of multiple stressors across consecutive reproductive stages, including stages not addressed here, can greatly enhance our ability to interpret trends and manage populations.

In this system where timing of important events is not necessarily closely coupled, phenological interactions in the form of timing mismatches could also have profound effects on reproductive success. Shultz *et al.* (2009) found that kittiwake phenology in Lower Cook Inlet, Alaska (400 km from our study site) is determined by early season food availability ("constraint" hypothesis) rather than by anticipation of peak forage availability for chick rearing ("anticipation" hypothesis) (Shultz et al. 2009). This linkage between early season conditions and the nesting schedule may allow mismatches to occur between kittiwake phenology and the timing of optimal prey availability for growing chicks, if optimal chick feed timing is not tightly coupled to early season conditions (e.g., Watanuki *et al.* 2009, Burthe *et al.* 2012). Our work adds a third phenological element, salmon run timing, which is not coupled to kittiwake phenology ($r = -0.08$) and that appears to have a profound effect on hatching success. With three timing components influencing reproductive success, the potential for mismatches increases dramatically.

Such patterns offer us a glimpse into the potential resilience of seabirds to changes in parameters affecting breeding success. Phenology, in particular, is changing for many kittiwake populations, with a trend toward later timing in the North Sea (Frederiksen et al. 2004a, Burthe et al. 2012) and earlier timing in the Bering Sea (Byrd et al. 2008), but no significant trend for kittiwakes in a European high Arctic colony (Moe et al. 2009). Our work, along with that of Renner et al. (2014) and Schultz et al. (2009) highlights the important role of phenology in determining kittiwake laying success. However, the buffering potential of early salmon run timing suggests that poor food availability during the early breeding season may not have consistent effects on reproductive success. Conversely, reduced food availability early in the breeding cycle due to overfishing (e.g., Frederiksen et al. 2004b) or climate shifts (e.g., Hunt Jr. et al. 2002) may impair the ability of seabird colonies to produce chicks during years with prolonged predation periods due to late salmon runs.

CONCLUSIONS

The International Panel on Climate Change predicts major transformations in sea surface temperatures, salinity levels, and ocean acidification in response to the rising concentration of greenhouse gases in the atmosphere (e.g. carbon dioxide, methane and ozone) (IPCC 2007) that will potentially shift species distributions, disrupt predator-prey interactions, impose new physiological constraints on organisms, and alter primary production levels (Sverdup et al. 1942; Mann 1993; Cox et al. 2000, Etherington et al. 2004; Sarmiento et al. 2004). In response, natural resource conservation and management strategies are shifting from species-specific approaches to ecosystem-based approaches

and marine spatial planning (e.g. United Nations Educational, Scientific, and Cultural Organization Marine Spatial Planning Initiative, Executive Order No. 13547, Magnuson-Stevens Reauthorization Act 16.US.C. § 1801(3)(3), NOAA Next-Generation Science Plan, U.S. Fish and Wildlife Service National Wildlife Refuge System), yet the relationships among organisms and between organisms and their physical environment are not yet well understood (Weimerskirch et al. 2003; Arkema et al. 2006; Leslie & McLeod 2007). Our limited understanding of complex ecological interactions hinders our assessment of biological dynamics of marine ecosystems and potential effects of large-scale environmental disturbances such as climate change (Griffies 2004).

Here we show that early stages of a seabird breeding cycle have the potential to react synergistically or antagonistically to stressors acting in concert. Our results support the idea that exposure to one stressor can degrade an organism's ability to deal with a second, and that, perhaps, alleviating pressure from one stressor could improve the organism's resilience to a second. Identifying and addressing such interactions can enhance the success of ecosystem management efforts in many systems. As climate change continues to alter multiple aspects of marine systems simultaneously, our predictive abilities will rely upon our ability to understand the effects of complex multivariate interactions on individuals, populations, and communities.

ACKNOWLEDGMENTS

For field assistance, we would like to thank Joe Albanese, Andrew Allyn, Emily Bernhardt, Karen Brenneman, Traci Caddy, Chelsea Effinger, Greg Golet, Max Kaufman, Laura Kennedy, Alex Robbins, Tanya Sandberg-Diment, Kelsey Sullivan, and

Gloria Zager and the many field volunteers that made this work possible. Funding for the original experiment was provided by the U.S. Fish and Wildlife Service, the *Exxon Valdez* Oil Spill (EVOS) Trustee Council, and the Earthwatch Institute. The U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit and the University of Maine provided administrative, financial, and computer resources support during data analysis and manuscript development. Steve Moffitt of the Alaska Department of Fish & Game (ADF&G) provided pink salmon run data; ADF&G is not responsible for errors or deficiencies in reproduction, subsequent analysis, or interpretation of salmon data. This study does not necessarily reflect the views of the EVOS Trustee Council, the Earthwatch Institute, or the U.S. Fish and Wildlife Service. Mention of trade names and commercial products does not constitute endorsement or recommendation for use by the U.S. Government.

CHAPTER 4: EXPERIMENTAL EVIDENCE OF LONG-TERM REPRODUCTIVE COSTS IN A COLONIAL NESTING SEABIRD

ABSTRACT

Trade-offs between current and future reproduction are central to the evolution of life histories. Experiments that manipulate brood size provide an effective approach to investigating future costs of current reproduction, as experimenters can control for individual traits such as quality and age. Most manipulative studies to date, however, have addressed only the short-term effects of manipulation. Our goal was to determine whether survival or breeding costs of reproduction in a long-lived species manifest beyond the subsequent breeding season. To this end, we investigated long-term survival and breeding effects of a multi-year reproductive cost experiment conducted on Black-legged Kittiwakes *(Rissa tridactyla),* a long-lived colonial nesting seabird. We used multi-state capture-recapture modeling to assess hypotheses regarding the role of experimentally reduced breeding effort and other factors on future survival and breeding probabilities during the 16-year period following the experiment. We found that forced nest failures had a positive effect on breeding probability over time, but had no effect on long-term survival, consistent with the demographic buffering hypothesis. This apparent canalization of survival suggests that adult survival is the most important parameter influencing fitness in this long-lived species, and that adults should pay reproductive costs in ways that do not compromise this critical life history parameter. When declines in adult survival rate are observed, they may indicate populations of conservation concern.

INTRODUCTION

Life history theory proposes that strategies evolve to maximize lifetime reproductive success, requiring organisms to balance a number of energetically costly activities, including growth, self-maintenance, and reproductive effort (Stearns 1992). Tactics for attaining this balance vary widely among organisms, as selective pressure for particular life history traits depend on environmental factors (Stearns 1976; Barbraud & Weimerskirch 2001; Bordsen *et al.* 2011), resource availability (Goss-Custard *et al.* 2006), predation risk (Reznick, Bryga & Endler 1990; Martin 1995), and density-dependent processes (Fowler 1981; Frederiksen & Bregnballe 2000), each of which are both variable and often unpredictable. Further, an organism's capacity for responding to these pressures may be limited by physical, ecological, and phylogenetic constraints (Gould & Lewontin 1979). The life history strategies of any organism therefore represent ongoing attempts to balance trade-offs in a way that will maximize individual fitness (i.e., an individual's genetic contribution to the gene pool relative to the average contribution in the population) under the conditions imposed by the organism's particular set of constraints.

For iteroparous organisms, trade-offs between current and future reproduction also shape life history strategies. Since Williams (1966) first proposed the existence of such trade-offs, reproductive costs (i.e., the reduction of future reproductive potential in favor of the current reproductive effort) have been documented across a variety of taxa including marine invertebrates (e.g., Fernández, Bock & Pörtner 2000), fish (e.g., van den Berghe 1992), amphibians (e.g., Ryser 1989), reptiles (e.g., Seigel *et al.* 1987), mammals

(e.g., Koivula *et al.* 2003), and birds (e.g., Erikstad *et al.* 1997; Veasey *et al.* 2001; Alonso-Alvarez *et al.* 2004).

Reproductive costs can reduce survival and subsequent breeding success, as reported in many taxa (e.g., Reid 1987; Boyd *et al.* 1995; Miles, Sinervo & Frankino 2000; Koivula *et al.* 2003; Blomberg *et al.* 2013), though the proximate mechanism is not always clear. While some reproductive cost mechanisms likely operate over short time scales, others may incur longer-term consequences. Over the short term, breeding can degrade body condition, especially in species that undertake parental care of offspring (Reid 1987; Golet, Irons & Estes 1998; Hanssen *et al.* 2005), with potential consequences for survival and the subsequent breeding attempt. Reproductive activity also can expose individuals immediately to increased predation risk (Magnhagen 1991), which may be further exacerbated by impaired mobility resulting from reproduction such as that caused by extra mass in gravid females (Seigel *et al.* 1987; Veasey *et al.* 2001; Kullberg *et al.* 2002). Beyond such direct and immediate costs, breeders may also pay indirect costs. For example, if breeding activity delays the molting period in birds, poor feather growth could affect subsequent survival (Dawson *et al.* 2000). Physiological effects of reproduction have the potential to affect breeders over even longer time scales. Breeding can reduce immune function (Hanssen *et al.* 2005), increase vulnerability to oxidative stress (Alonso-Alvarez et al. 2004), and cause deleterious changes in other physiological processes such as calcium metabolism and cell growth regulation (Plumel *et al.* 2014). Such physiological changes could potentially carry lifelong consequences, but to date, there have been few investigations into long-term costs of reproduction in wild populations.

Short-term costs to survival and subsequent reproduction have been well-documented in a number of species, but few studies test for costs persisting beyond the following breeding season. Long-term investigations have been confined to observational studies of wild populations, where long-term costs of reproduction can be confounded by heterogeneity in quality (i.e., variation in underlying survival probabilities and reproductive potential) among individuals. For example, mean reproductive success can increase with age among long-lived birds (e.g., Ollason & Dunnet 1978; Sydeman *et al.* 1991; Green 2001); however, this trend likely results from selective removal of lower quality individuals over time (Cam *et al.* 2002; Aubry *et al.* 2009; Lescroel *et al.* 2009), which causes an apparent increase in reproductive success with age (Cam & Monnat 2000). Better quality individuals may secure more resources or use them more efficiently, allowing them to both survive and reproduce better than lesser quality counterparts (van Noordwijk & deJong 1986). Manipulative experiments, when feasible, are a superior approach for investigating reproductive costs, as experimenters can control for individual heterogeneity and other confounding factors using random assignment of treatments and controls. Although there have been a number of short-term reproductive cost experiments (e.g., *songbirds:* Parejo & Danchin 2006; *waterfowl:* Lessels 1986; *seabirds:* Velando & Alonso-Alvarez 2003), we have found no results from long-term (i.e., >1 year) experimental assessments.

Our goal in this study was to determine experimentally whether survival or breeding costs of reproduction in a long-lived species manifest beyond the subsequent breeding season. We were particularly interested in discerning among four possible hypotheses regarding long-term reproductive effects: 1) reproductive costs occur only

over the short-term (no long-term effects are detectable); 2) long-term reproductive costs involve breeding potential only; 3) long-term reproductive costs involve survival only, and 4) long-term reproductive costs affect both breeding potential and survival. To distinguish among these potential outcomes, we analyzed a multi-decade monitoring database of Black-legged Kittiwakes *(Rissa tridactyla;* hereafter "kittiwakes") involved in a four-year manipulative reproductive cost experiment at an Alaskan colony in the early 1990s. See Golet, Irons & Estes (1998), Golet & Irons (1999), and Golet *et al.* (2004) for results of studies assessing short-term costs. We used multi-state capture-mark-recapture modeling (Nichols & Kendall 1995) to quantify survival and breeding probabilities based on state-specific (breeding vs. non-breeding) encounter and transition probabilities, and used individual covariates to incorporate factors affecting survival and breeding decisions. We used this approach to evaluate whether differing degrees of forced non-breeding over four successive years had persistent effects on survival or breeding probability over the following 16 years.

METHODS

Focal species

The kittiwake is a small, long-lived (mean life expectancy at a North Pacific colony = 13 years; Hatch, Roberts & Fadely 1993), piscivorous gull with a circumpolar distribution throughout the northern hemisphere and a global population size estimated to be from 17 to 18 million individuals (Delany & Scott 2006). Kittiwakes are colonial cliff-nesters, rearing one, two, or rarely three young per breeding season. As in many seabird species, both parents share incubation and chick-rearing duties equally (Coulson &

Wooller 1984). Both mate- and nest-site fidelity are high (Coulson & Thomas 1985), facilitating long-term capture-recapture studies and studies of life history evolution.

Site description

The Shoup Bay kittiwake colony is located in northeastern Prince William Sound (PWS), Alaska (61° 10' N, 146° 35' W; Fig. 4.1). Shoup Bay is a fjord that adjoins Port Valdez with a tidewater glacier that terminates at the bay's western end. The bay connects to Prince William Sound via a reversing tidal river ~ 0.75 km in length. During the early years of our study the bay was frequently filled with large icebergs calved from the glacial face, until the late 2000s, when the glacier retreated mostly onto land. The kittiwake colony is located primarily on the south-facing side of a rocky island ~0.4 km in length and ~100 meters from the mainland. Based on annual nest counts, colony size peaked in 2002 with 19,000 actively breeding birds, but declined to 14,400 active breeders by 2010, the final year of this study (Irons, unpublished data). While predation was substantial during some years, the majority of predation occurred following the period when we resighted marked individuals at the colony, and thus did not appreciably influence non-breeding status assignments. Predators at the colony are predominantly avian and include bald eagles *(Haliaeetus leucocephalus),* peregrine falcons *(Falco peregrinus),* common ravens *(Corvus corax),* northwestern crows *(Corvus caurinus),* and black-billed magpies *(Pica hudsonia).* Occasional mammalian predators include American mink *(Neovison vison)* and wolverine *(Gulo gulo).*

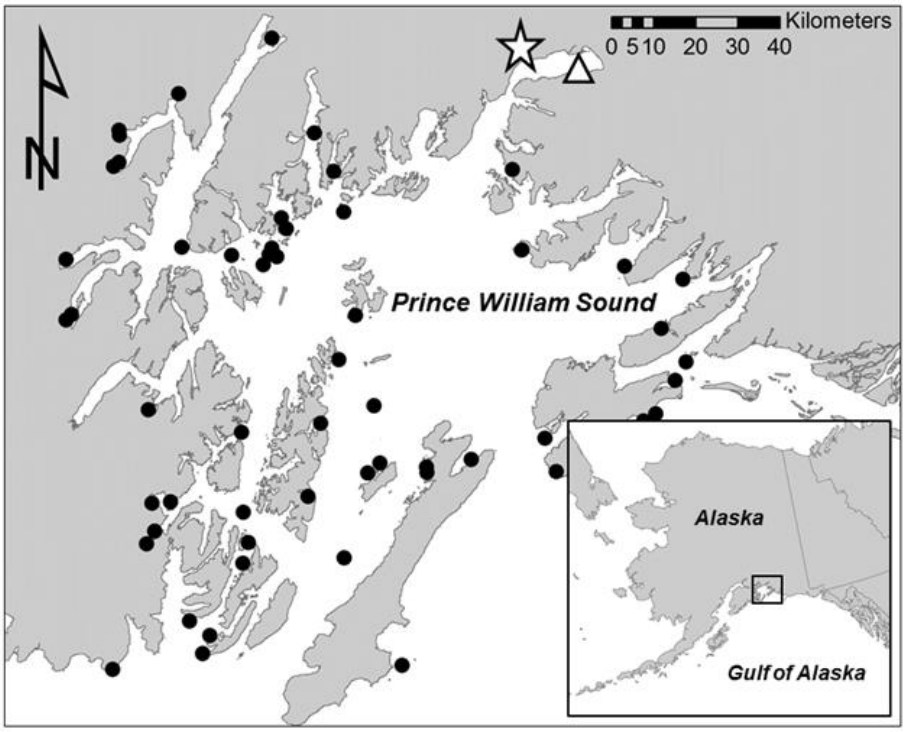

Figure 4.1. Kittiwake colony locations. Location of the Shoup Bay kittiwake colony (star), the Alyeska Pipeline Terminal colony (triangle) and all other kittiwake colonies (circles) ever reported in the Prince William Sound region, Alaska (NPSDP 2015), most of which were active during some or all of the 20 year study period. Inset map shows the location of Prince William Sound within Alaska.

Original cost of reproduction experiment

We examined long-term survival and breeding trends for kittiwakes included in a multi-year cost of reproduction study during the early 1990s (Golet, Irons & Estes 1998; Golet & Irons 1999; Golet *et al.* 2004). In 1991, 850 adult kittiwakes were captured at the Shoup Bay colony and each was marked both individually (right leg) and as a member of the study cohort (left leg) with a combination of colored Darvic leg bands and a numbered steel federal leg band (six bands in total). Captured birds had adult plumage and were at least two years of age at the time of capture. During 1991 – 1994, between

162 and 270 active nests were randomly selected each year from this group for late-stage egg removal to evaluate the short-term costs of reproduction. Naturally occurring costs were assessed by comparing birds raising their natural clutches with those that had their entire clutches removed. Golet *et al.* (1998; 1999; 2004) used several measures to minimize bias resulting from individual heterogeneity within the sample population. Manipulation samples included nests with the same proportion of one- and two-egg clutches as the larger population. Further, the random sampling process ensured that the manipulated and non-manipulated breeders shared similar distributions of age structure and individual quality to the population as a whole. Detailed methods for the manipulative study are provided in Golet *et al.* (2004). Although some experimental nests were attended by two marked birds, potentially violating independence assumptions, we included both members of each pair in our analysis for reasons discussed in Golet *et al.* (2004). For the present study we included only individuals that were encountered at least once following completion of the manipulative experiment in 1994.

Data collection

From 1995 through 2010, crews of four to eight observers used binoculars and 20-60X spotting scopes to resight color-banded birds during mornings and evenings in May when breeders were actively building nests. Major nesting sections (N=10) were delineated using cliff features, and birds were resighted within each section an average of 9.8 (± 0.7; 95% CI) times throughout the nesting season, though resighting effort was reduced in the final two years of the study owing to personnel and environmental limitations (mean number of observation sessions 2009-2010 = 4.2 – 6.2; 95% CI). We

were unable to examine the nest contents of each bird to determine breeding status, so we relied on proxy observations to designate breeding status for individuals during each year. These were based on the number of times individual birds were recorded at a particular nest site. Birds seen three or more times at a single nest site were considered to be likely breeders ("breeders" hereafter), whereas birds sighted ≤2 times at a single nest site or seen only outside of a nest patch were considered to be likely non-breeders ("non-breeders" hereafter). These criteria allowed us to effectively designate birds actively engaged in breeding from those present at the breeding colony but not regularly attending a nest site. We also surveyed a nearby (15 km) kittiwake colony at the Alyeska pipeline terminal dock twice in 2007 to document permanent emigration of Shoup colony breeders, which could bias estimates of survival.

Some bands faded, overlapped, or were lost during the study, which violated basic capture-mark-recapture assumptions of permanent markings. We addressed this issue by adopting a "time-varying mark" approach similar to that used in mammalian camera-trap studies (e.g., Negroes *et al.* 2010), where associations between bird identity and band combination were allowed to change over time. We manually reconstructed individual histories for birds with compromised band combinations using a variety of clues, including presumed mate identity, nest site location, capture records, partial reads of band serial numbers, and unique physical characteristics. Using these methods, we were able to effectively reconcile the majority of degraded individual band combinations in each year. We could not account for cohort mark loss, which could lead to underestimation of survival probabilities; however, such loss was far less common due to the stabilizing influence of the steel band placed between the two Darvic bands on the left leg. We have

no reason to suspect that mark degradation was confounded with our manipulation categories, and therefore it should not affect our conclusions regarding the effects of manipulation on survival and breeding probability.

Multi-state modeling

We used multi-state models (Nichols & Kendall 1995) to assess the long-term effects of manipulation frequency on demographic parameters in the kittiwake. Multi-state modeling allowed us to simultaneously estimate apparent survival probability (ϕ), resighting probability (p), and the probability of transitioning between pre-defined states (ψ), in this case breeding and non-breeding. The probabilities of transitioning to the non-breeding state were estimated by maximum likelihood, and the transitions to the breeding state were calculated through subtraction.

Because all individuals were marked prior to the beginning of this study, we allowed all birds to enter the capture history as assumed breeders during 1994, the year prior to our post-manipulation period, to simplify modeling. We then fixed the first year survival to 1.0, the probability of transitioning from non-breeder to breeder to 0.0, and the probability of remaining in the breeding state in year 2 to 0.82, as estimated by the model with full state*time dependence.

We incorporated several environmental variables likely to affect annual survival or breeding probability that were unrelated to the experimental design. We included these as covariates in the modeling process (Table 4.1). Pacific Decadal Oscillation (PDO) driven regime shifts affect seabird population dynamics in the Gulf of Alaska (e.g., Hatch 2013); therefore, we obtained PDO index values (1995 – 2010) (JISAO

2015) and applied the average monthly PDO from October - March as an effect on the following season's demographic parameters. Further, because breeding decisions may be affected by conspecific success in the previous year (Danchin, Boulinier & Massot 1998), we also incorporated the previous year's annual colony productivity (total number of chicks fledged per total nests built over the entire colony) as an effect on subsequent year breeding probability. Both environmental variables were z-standardized (mean = 0.0, SD = 1.0) prior to analysis.

Although the experimental nature of our study reduced confounding effects of individual heterogeneity, one potential source of heterogeneity remained. Golet et al. (1998; 1999; 2004) manipulated birds over four years in late-stage incubation and compared those birds to non-manipulated individuals that also had eggs during this period. For our analysis, we defined breeding cost as the inverse of manipulation frequency over the four years, but in doing so we do not account for individuals that skipped breeding and were therefore unavailable for manipulation during some years. Because better quality individuals were more likely to breed consistently (Cam et al. 1998), they were also more likely to receive repeated manipulations than poorer quality individuals. We accounted for this source of possible heterogeneity by differentiating those individuals known to have nested (i.e., eggs were detected) in all four years of the manipulation from those known to have at skipped reproduction at least once. We will refer to these two groups as good and poor quality, respectively. Birds with unknown breeding status during one or more years were designated as unknown quality. We applied this three-factor variable as a covariate and tested its effect on both demographic parameters. Because the variable describes breeding status prior to the focal time period

of our study, it is does not inherently conflict with the state designations we used for our analysis. We assessed the persistence of the quality effect by examining the 1995-1998 breeding frequency in non-manipulated good and poor quality breeders known to have survived through this period. Sex could not be determined for all individuals, so we did not include sex as a covariate.

We used a sequential approach to develop and compare a set of candidate models following Blomberg *et al.* (2013), where we accounted for fundamentally different sources of variation during each stage of analysis. We first considered temporal variation by fitting models with all temporal variables (i.e., year, time period, time trend, PDO, productivity) and retaining the best-supported model structure contrasted with a null model. We then considered non-temporal variables as additive effects to our best-supported temporal structure, again retaining variables that improved model fit. Finally, we considered potential interactions between variables.

We conducted our analyses in these three stages to determine the most parsimonious model structure for each of our three parameter types, ϕ (survival probability), p (encounter probability), and ψ (transition probability). We first constructed a set of resighting probability models, while allowing a fully general (i.e., with full time and state dependence) model structure for survival and transition probabilities. We then applied the best resighting structure to the candidate set of transition models with fully general survival structure. Finally, we used the best resighting probability structure and a fully general transition probability structure to build candidate models investigating factors affecting survival. This approach ensured that the constraints were applied only to the reproductive cost (survival, breeding) of interest, allowing the differences among

models to represent the hypothesized patterns in this parameter alone (as in Golet *et al.* 2004). We considered any model structure to be competitive if it successfully converged, if the confidence intervals of beta estimates associated with the model's core hypothesis did not overlap 0, and if $QAIC_c$ scores fell within 2.0 units of the best model from the candidate set in question.

We used $QAIC_c$ model selection procedures to evaluate support for competitive models (Burnham and Anderson 1998). We assessed goodness-of-fit of the most general model (with resight, survival, and transition structures all set to full state * time dependence) with the general "Jolly-Move" (JMV) model in Program U-CARE (Choquet *et al.* 2009). We used the test results to calculate a variance inflation factor and adjusted AIC_c values to $QAIC_c$ accordingly for the entire model set (Choquet *et al.* 2009). We performed all other demographic modeling with Program MARK (White & Burnham 1999). For models with full annual time structure in both p and ϕ or ψ, we avoided interpretation of parameter estimates for the final time period, for which survival/transition and resight probabilities are confounded. We report 85% confidence intervals for all parameter coefficients, as the 85% confidence level is more compatible with model AIC selection than the more traditional 95% confidence intervals, which may overlap 0.0 for coefficients whose inclusion is otherwise supported by AIC selection (Arnold 2010). We considered our long-term reproductive cost hypothesis supported when top-ranked models included the manipulation term and that term had a significant positive effect on survival or breeding probability.

Sensitivity analyses

We performed sensitivity analyses to evaluate data processing decisions regarding tag loss and breeding state designations. We evaluated the possible bias associated with band misclassification issues with a sensitivity analysis in which we duplicated the major components of our analyses with and without individuals with time-varying marks. We likewise evaluated the effect of breeding state designations, which were based on repeat sightings at a single nest site. We did this by comparing the analysis results when both two- and three-sighting criteria were used to identify breeders.

RESULTS

We modeled data from 664 kittiwakes that were marked in 1991 in the original cost of reproduction experiment. In each year, 29.8 – 39.4% (95% CI) of individuals known to belong to the experimental cohort had some form of mark degradation (missing or overlapped color bands); we were able to identify 65.7 – 78.1% (95% CI) of these birds using our time-varying mark technique. Our resighting activity at the neighboring Alyeska Pipeline colony (population size 9,200 breeders in 2007; Irons, unpublished data), the closest (<10 km) of the more than two dozen kittiwake colonies located within Prince William Sound, suggested that emigration was negligible among experimental birds: out of 2,022 adults banded at the Shoup colony between 1988 and 2006, only six individuals were resighted at the Alyeska Pipeline colony in 2007, and none of these were members of the experimental cohort (both manipulated and control birds). Similarly, no members of the experimental cohort were resighted at the Clove Triangle colony (85 km from Shoup Bay) or the North Icy Bay colony (135 km from Shoup Bay)

during intenstive resighting efforts in 1997 and 1998 associated with the Alaska Predator Ecosystem Experiment. Based on breeding behavior during the initial experiment, 235 individuals (35.4%) were designated as good quality, 267 (40.2%) were poor quality, and 162 (24.4%) were of unknown quality (Table 4.2). Among unmanipulated breeders surviving at least through 1998, subsequent breeding in 1995-1998 was greater in good quality birds (average 3.4 ± 0.4 seasons, N = 20) than in poor quality birds (2.6 ± 0.3 seasons, N = 94; birds of unknown quality = 2.1 ± 0.29 seasons, N = 50). Because nests were selected for experimental clutch removal at random from available breeders each year, most birds experienced 0 or 1 forced nest failure, whereas fewer birds experienced 2, 3, and 4 forced failures, respectively (Table 4.1). Return rates declined over time; of 664 individuals known to be alive in 1995, 55 were resighted in 2010 (Fig. 4.2). Without factoring in detection probability, this return rate corresponds to an annual survival rate of 0.86.

The UCARE goodness-of-fit test of the most general model indicated a moderate degree of overdispersion, likely due in part to the unbalanced nature of the marking process (all individuals marked on occasion one); we therefore adjusted all AIC_c to $QAIC_c$ with the estimated variance inflation factor $\hat{c} = 2.9$. The best-supported model structure for resighting probability included only state dependence ($w_i = 1.0$; Table 4.3) where resight probability was 1.0 for individuals in the breeding state, and was 0.46 (0.02 SE) for the non-breeding state. We applied this structure on all subsequent models. The best performing model structure for survival contained an additive effect of state and a linear time trend, but did not contain a manipulation effect ($w_i = 0.33$; Tables 4.4, C1, C2). This model suggested that breeders experienced significantly greater survival

probabilities than did non-breeders, and that survival probability decreased significantly over time for individuals in both states (Fig. 4.3). While several covariate models also were competitive, parameter coefficient confidence intervals overlapped 0.0 for PDO, manipulation, and productivity variables in these models, indicating lack of support for these effects. In contrast, the best-supported model of state transition ($w_i = 0.59$) included an interaction between state and year and an additive manipulation effect (Tables 4.5, C3, C4). Regardless of manipulation category, the model suggested that the probability that a breeder would transition to the non-breeding state increased relatively steadily until 2005, after which it declined steeply (Fig. 4.4). The manipulation coefficient for the top-ranked model indicated that manipulation had a negative effect on the probability of future non-breeding (β_{manip}= -0.22 – -0.04; 85% CI); in other words, forced nest failures led to a lower propensity for skipping breeding that persisted for many years following the initial manipulation (Figs 4.4 & 4.5). The second-ranked transition model ($w_i = 0.21$, $\Delta QAIC_c = 2.06$) included an additive effect of binary manipulation category that also suggested manipulation increased later breeding probability (β_{cmanip}= -0.60 – -0.04; 85% CI). All told, models incorporating a manipulation effect had a cumulative Aikake weight of $w_i = 0.80$.

Sensitivity analyses

Both sensitivity analyses yielded results consistent with the primary modeling analysis: no manipulation effect on survival, and a significant negative manipulation effect on the probability of skipped breeding. The dataset with degraded marks removed included records for 434 individuals. We adjusted AIC_c to $QAIC_c$ using a variance

Table 4.1**.** Multi-state modeling variables. Variables included in multi-state models of kittiwake survival and breeding probability in the 16 years following a four-year reproductive cost experiment in which late-stage eggs were removed from randomly selected nests at the Shoup Bay colony, Prince William Sound, Alaska.

Category	Variable	Description
Encounter data	*Encounter history*	Individual resighting histories (1995-2010)
State	*State*	Breeding: resighted 3 or more times at the same nest site Nonbreeding: resighted <3 times at the same nest site
Temporal variables	*Time*	Year (1995 - 2010)
	Period	Early: 1995-1999 Mid: 2000-2004 Late: 2005-2010
	Trend	Linear increase or decrease over time
	Prod	Total annual colony productivity in previous year
	PDO	Average Oct-Mar Pacific Decadal Oscillation index value for previous winter
Individual variables	*Manip*	Manipulation (continuous): Number of years of forced nest failures 1991-1994 (0 - 4)
	Cmanip	Manipulation (categorical): Low -- forced nest failure in 0 - 2 years High -- forced nest failure in 3 - 4 years
	Qual	Quality: Good -- known breeders 1991-1994 Poor -- skipped 1+ breeding season 1991-1994 Unknown -- never known to skip a season, but at least 1 unknown state 1991-1994

Table 4.2. Sample sizes by manipulation and quality categories. Breakdown of sample sizes by manipulation category and individual quality (based on breeding frequency in 1991-1994, see Table 4.1) for experimental kittiwakes seen at least once between 1994 and 2010 at the Shoup Bay colony in Prince William Sound, Alaska. During 1991-1994, nests were selected at random each year for experimental manipulation from the pool of available marked breeders; individuals therefore experienced forced nest failure during late stage incubation in 0, 1, 2, 3, or 4 years.

Manipulation years	**Individuals**	**Individual quality [N (%)]**		
		poor	*unknown*	*good*
0	210	118 (56.2)	65 (31.0)	27 (12.9)
1	249	99 (39.8)	58 (23.3)	92 (37.0)
2	142	42 (29.6)	29 (20.4)	71 (50.0)
3	57	8 (14.0)	10 (17.5)	39 (68.4)
4	6			6 (100.0)

Table 4.3. Resight probability model performance. Performance of competing multi-state models estimating the probability of resighting for black-legged kittiwakes with respect to breeding state at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010. Model structure for survival and transition probabilities was held constant as state*year. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis.

Model	**Hypothesis**	**$\Delta QAIC_c$**	**w_i**	**K**
$p_{(state)}$	Resight probability varies only in relation to breeding state.	0.00	1.00	64
$p_{(state + time)}$	Resight probability varies between breeding state and among years.	12.80	0.00	79
$p_{(state \times time)}$	Resight probability varies between states and among years, with a different yearly pattern of resighting probability between states.	40.38	0.00	94
$p_{(time)}$	Resight probability varies only among years.	195.11	0.00	78
$p_{(constant)}$	Resight probability does not vary.	262.36	0.00	63

Table 4.4. Survival probability model performance. Performance of competing models with ΔQAIC < 7.0 for multi-state models estimating the probability of survival (φ) for black-legged kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010. Model structure for transition probability was held constant as state*time, and resight model structure was set to the best competing structure from Table 4.3. Full results table for all survival models is available in the Supplementary Information (Table C1). Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
$\varphi_{(state + trend)}$	Survival varies between states with a trend over time.	0.00	0.33	34
$\varphi_{(PDO + state + trend)}$	Survival varies between states and among PDO index values with a trend over time. PDO is a time-varying value common to all individuals within each year.	0.19	0.30	35
$\varphi_{(manip + state + trend)}$	Survival varies between states and between treatment groups with a trend over time.	1.93	0.13	35
$\varphi_{(prod + state + trend)}$	Survival varies between states and among colony productivity values with a trend over time. Colony productivity is a time-varying value common to all individuals within each year.	1.98	0.12	35
$\varphi_{(qual + state + trend)}$	Survival varies between states and among quality categories with a trend over time.	2.82	0.08	36
$\varphi_{(state X period)}$	Survival varies between states and among early, mid-, and late post-experimental periods, with a different period pattern between states.	6.56	0.01	36

Table 4.5. Breeding state transition probability model performance. Performance of competing models with ΔQAIC < 7.0 for multi-state models estimating the probability of transition (Ψ) between breeding and non-breeding states for Black-legged Kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010. Model structure for survival was held constant as state*time, and resight model structure was set to the best competing structure from Table 4.3. Full results table for all state transition models is available in the Supplementary Information (Table C3). Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
$\Psi_{(manip + state\ X\ time)}$	Nonbreeding varies between treatment groups, between breeding states, and among years, with a different yearly pattern between states.	0.00	0.59	62
$\Psi_{(cmanip + state\ X\ time)}$	Nonbreeding varies between binary treatment categories, between breeding states, and among years, with a different yearly pattern between states.	2.06	0.21	62
$\Psi_{(state\ X\ time)}$	Nonbreeding varies between breeding states, among years, and with a different yearly pattern between states.	2.57	0.16	61
$\Psi_{(quality + state\ X\ time)}$	Nonbreeding varies among birds of different quality, between breeding states, and among years, with a different yearly pattern between states.	5.43	0.04	63

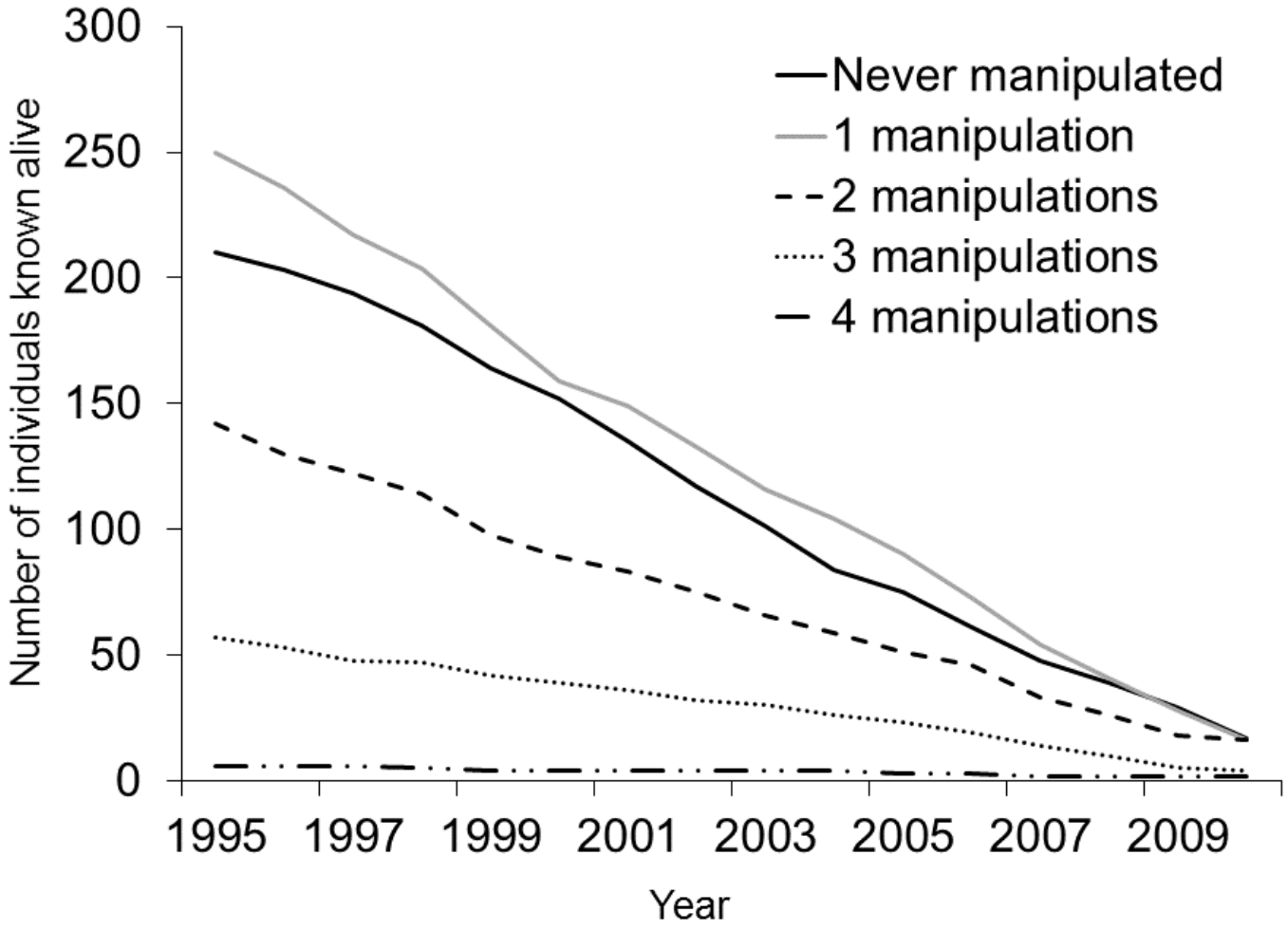

Figure 4.2. Known returns of experimental birds. Number of individual kittiwakes from the original cost of reproduction study known to still be alive in the 17 years following the conclusion of the original reproductive cost experiment (Golet et al. 2004), grouped by the number of forced nest failures experienced.

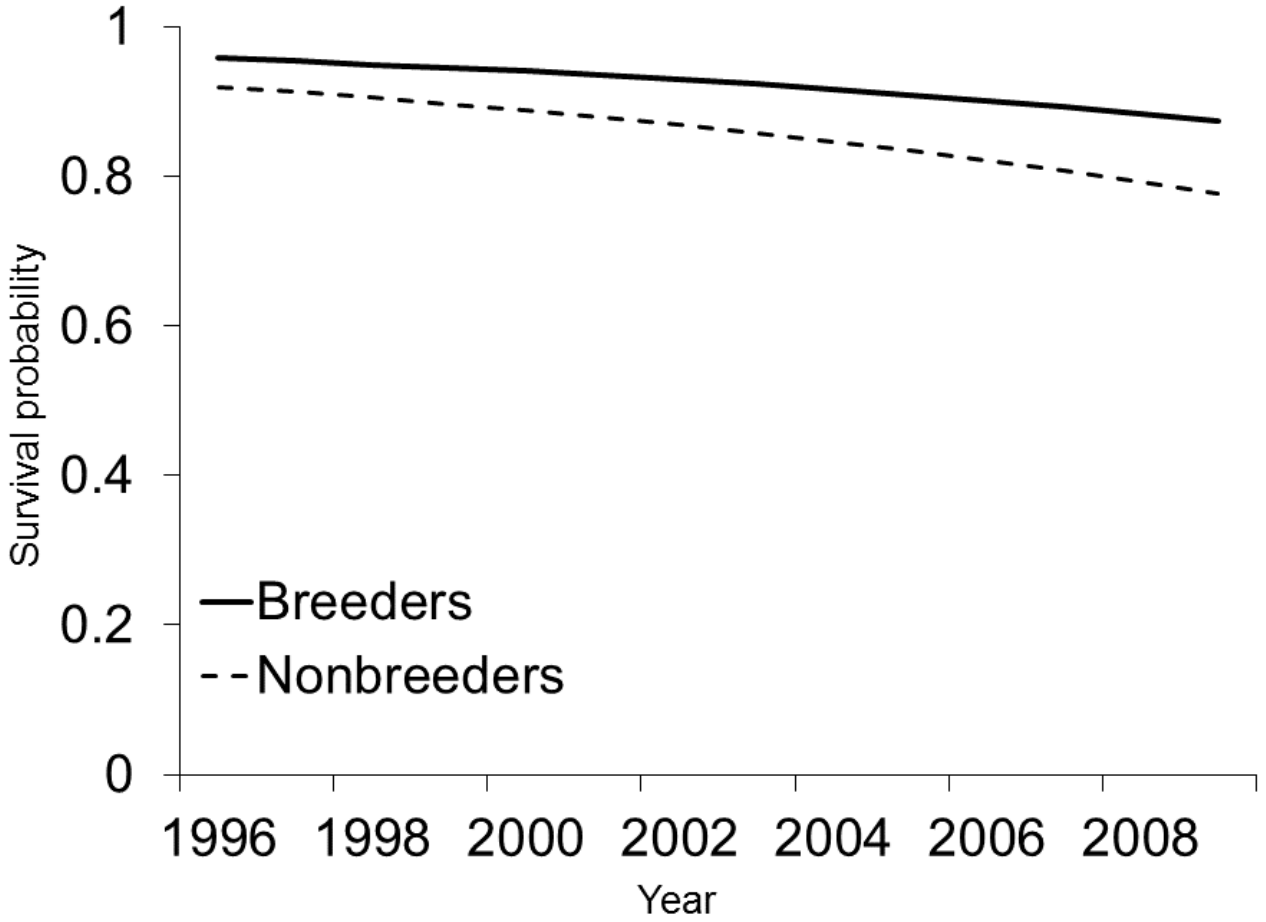

Figure 4.3. Survival probabilities from top survival model. Yearly survival probabilities for Shoup Bay, AK kittiwakes in breeding and non-breeding states, from the best multistate model structure for survival.

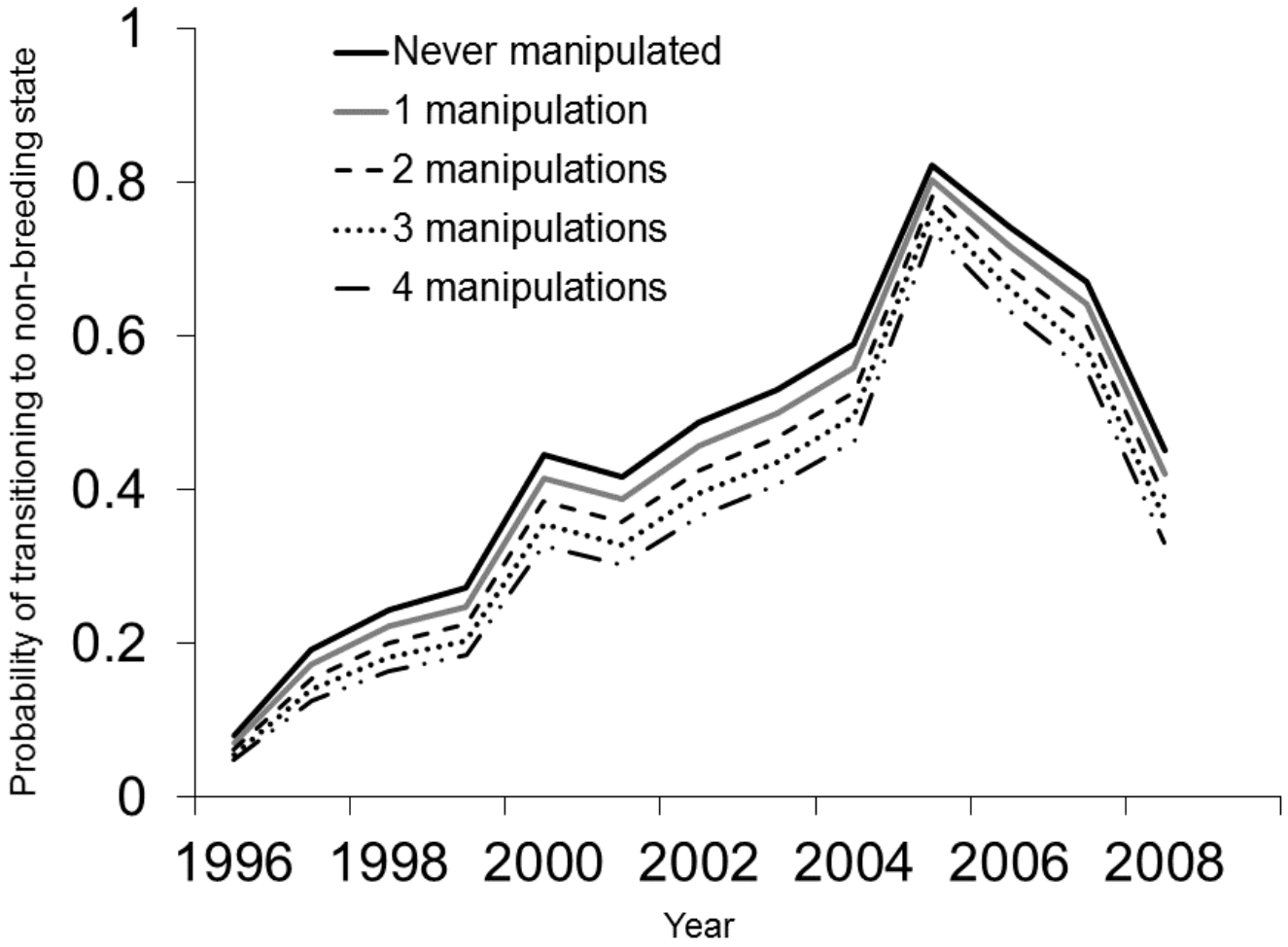

Figure 4.4. Breeder transition probabilities from top transition model. Annual probabilities of transitioning from a breeding to a non-breeding state for Shoup Bay, Alaska, kittiwakes by the number of experimentally forced nest failures during 1991-1994, from the best multistate transition model structure.

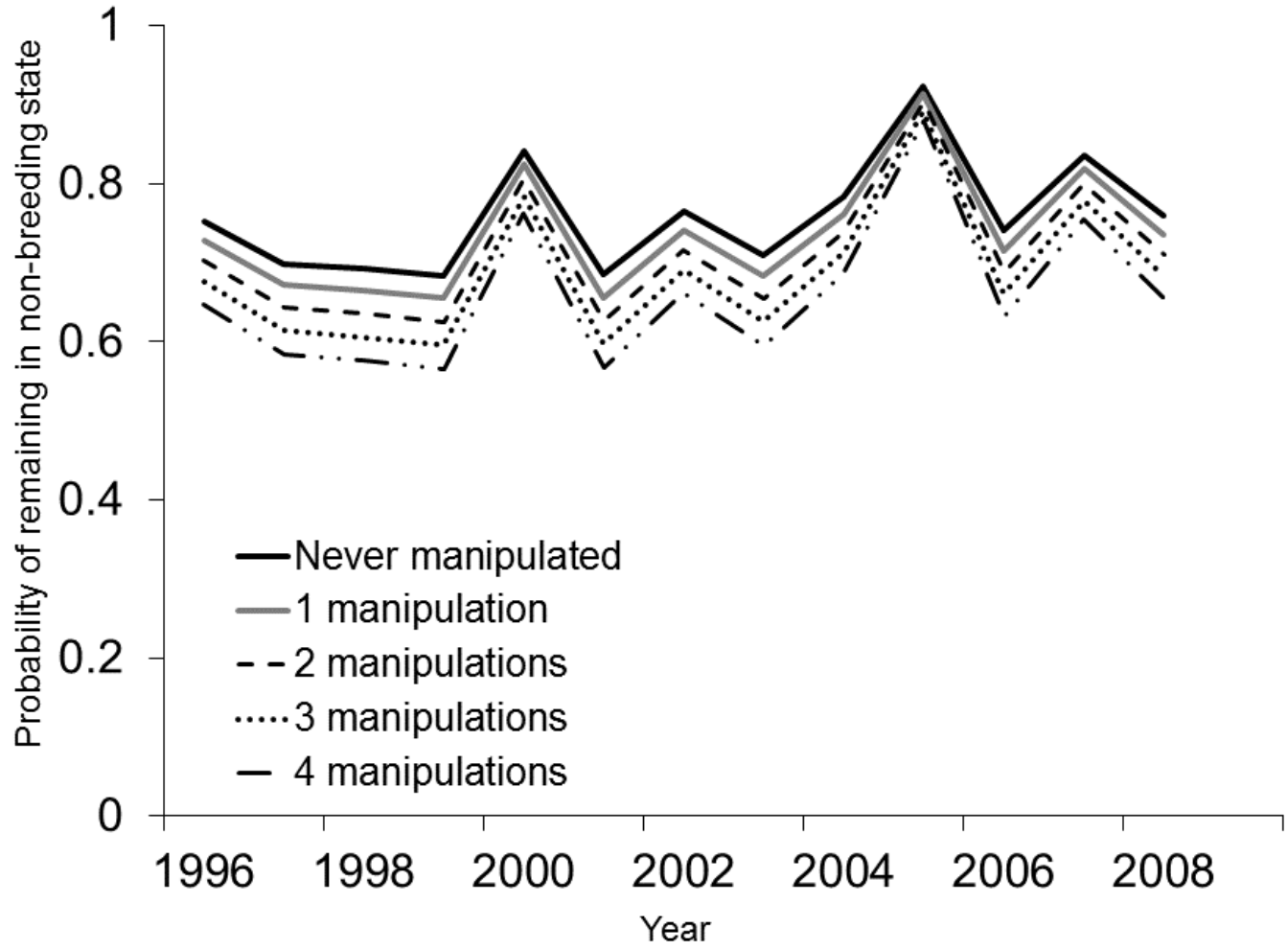

Figure 4.5. Non-breeder transition probabilities from top transition model. Yearly probabilities of remaining in a non-breeding state for Shoup Bay, Alaska, kittiwakes by the number of experimentally forced nest failures during 1991-1994, from the best multistate transition model structure.

inflation factor of 2.90. Resight probability model ranks were identical to the original analysis (Table C5). The top survival model ($w_i = 0.29$) included additive effects of state and time, rather than state and time trend as in the original analysis. However, there was no support for an effect of manipulation on survival; while an additive manipulation effect was included in the second- and fourth-ranked models ($w_i = 0.12$, $\Delta QAIC_c = 1.81$ and $w_i = 0.10$, $\Delta QAIC_c = 2.06$, respectively), the 85% confidence interval for the manipulation coefficients included 0.0 (Table C6). While the top transition model ($w_i = 0.42$) did not include the manipulation term, the second-ranked model ($w_i = 0.24$, $\Delta QAIC_c = 1.12$) was competitive and included a significant negative effect of manipulation on future breeding propensity (Table C7). For the sensitivity analysis on breeding state designations, we reclassified breeding status according to a two-sighting criteria in the full dataset (N = 664). We adjusted AIC_c to $QAIC_c$ using a variance inflation factor of 2.21. Resight probability model ranks were identical to the original analysis (Table C8). The top survival model included additive effects of state and time trend as in the original analysis. Again, there was no support for an effect of manipulation on survival; while an additive manipulation effect was included in the fourth- and fifth-ranked models in the competitive suite ($w_i = 0.11$, $\Delta QAIC_c = 1.88$ and $w_i = 0.10$, $\Delta QAIC_c = 1.99$, respectively), the 85% confidence interval for the manipulation coefficients included 0.0 (Table C9). In contrast, the top two transition models included a significant negative effect of manipulation on future breeding propensity ($w_i = 0.53$ and $w_i = 0.27$, $\Delta QAIC_c = 1.37$, respectively). As in the main analysis, models containing manipulation terms represented a cumulative weight of 0.80. We opted to retain individuals with time-varying marks in the full analysis, because the full dataset provided

a larger sample size, and we likewise retained the three-sighting criterion in keeping with the convention utilized in other work at the Shoup colony.

DISCUSSION

This investigation is the first we are aware of to document long-term demographic effects of brood size manipulation in a long-lived species. We found that experimental reduction in breeding effort resulted in greater breeding probability later in life, but not decreased mortality risk. Repeated forced nest failures were associated with increased probability of breeding later in life, in agreement with short-term (i.e., one-year time window or less) breeding effects documented in other studies (e.g., *capital breeders:* Lessels 1986; Hanssen et al. 2005; *income breeders:* Wernham & Bryant 1998; Golet *et al.* 2004, *but see* Pettifor 1993). Although Golet *et al.* (2004) documented a short-term survival cost of reproduction in the same cohort investigated here, we found no long-term effect of manipulation on survival. This suggests that in kittiwakes reproductive effort may incur short-term survival costs, but the brunt of the long-term cost is borne out by reductions in future fecundity rather than survival. Thus, survival is buffered at the expense of breeding effort, supporting the demographic buffering hypothesis.

Demographic buffering

Demographic buffering is caused by selection for alleles that result in population-level parameters resistant to the effects of environmental change. In long-lived taxa, demographic buffering favors stability in the life history trait with the greatest influence on individual fitness, at the expense of greater variability in other, less influential traits

(e.g., Gaillard & Yoccoz 2003, but see Barraquand *et al.* 2014). The premise behind demographic buffering is that variation in short-term fitness leads to a reduction in long-term fitness. Thus, adaptations that maximize the fitness of their carriers by maximizing the most important demographic parameters over diverse environmental circumstances are more likely to spread than similar adaptations in less important parameters. Life history tradeoffs between these adaptations prevent both from occurring. This concept stems directly from the mathematical behavior of population growth formulae (e.g., Lewontin & Cohen 1969; Gillespie 1977) under the assumptions that fitness (and therefore population growth of individuals with a particular phenotype) has a linear relationship with the dominant environmental variable, and that environmental variability is both random and stationary. The demographic buffering hypothesis therefore posits that organisms have evolved to absorb the effects of environmental stochasticity through variability in the demographic parameters that have the least influence on fitness. Most investigations into demographic buffering have used λ, the asymptotic population growth rate, as a proxy for fitness. Using this population-level proxy for an individual-level parameter assumes that the fittest alleles are prevalent in the population; however, this assumption would not be met for a population in the process of adapting to changing conditions. Further, great care must be taken to account for individual heterogeneity within the study population whenever population-level parameters are interpreted with respect to individual strategies.

Many studies have shown canalization (i.e., production of the same phenotype over a variety of environmental conditions) in the parameters with the greatest effect on λ (e.g., Pfister 1998; Saether & Bakke 2000; Gaillard & Yoccoz 2003). Our results suggest

that kittiwake survival may be similarly resistant to change ("canalized") over long time periods. Short-term survival costs theoretically could be explained by direct costs of reproduction, such as reversible changes in body condition owing to the energetic requirements of chick-rearing; however, body condition was only weakly correlated with the short-term survival effect (Golet *et al.* 2004). It is possible that it simply takes an individual some time to redirect indirect and physiological costs away from the canalized parameter. Alternatively, the observed short-term survival effect could arise from continued reproductive costs occurring outside of our monitoring period at the breeding colony. For example, post-fledging parental care in kittwakes (Mulard & Danchin 2008) may increase predation risk for successful parents.

Alternative hypotheses

It is also possible that the breeding effect in our study stems from a failure to account fully for individual heterogeneity within the sample population; however, this possibility is unlikely. The quality covariate failed to add sufficient explanatory power to survival and transition models, so we concluded that manipulation was random with respect to any underlying quality. Further, we suspect that age-based heterogeneity could have biased our results *against* detecting long-term survival and breeding costs. The initial captures likely included a number of young prospecting birds who were roosting in the capture locations. As young birds are less likely to breed, such birds may have been ineligible for manipulation during the early years and therefore may not have been as well-represented in the frequent manipulation categories, leading to a difference in age across manipulation groups. We would expect this age bias to result in reduced survival

and breeding over time among manipulated birds as older, more manipulated birds dropped out. Instead, we saw the opposite breeding effect, where more manipulated birds actually had greater breeding probabilities over the long term. Further, because quality has a well-known effect on survival (e.g., Cam *et al.* 1998), if quality were driving the relationship between manipulation and breeding probability, we might expect to see a similar relationship between manipulation and survival probability, which we did not detect in our analysis. These patterns, combined with the lack of explanatory power of our quality covariate, lead us to believe that the manipulation effect is likely real.

Another intriguing possibility is that the manipulation effect could stem not from cost deferment, but from an increased willingness to accept risk later in life in order to compensate for early reproductive failures. This requires an adjustment of breeding effort; however, this is known to occur in some long-lived seabirds. At least some species show senescent declines in foraging performance (e.g., Catry *et al.* 2006), yet continue to breed, apparently opting to sacrifice survival to buffer reproductive success as their future breeding opportunities dwindle (e.g., Heidinger, Nisbet & Ketterson 2006; Velando *et al.* 2006). Indeed, our results show a precipitous drop in skipped breeding in the final years of the study (when the minimum age of birds was 18 years), suggesting a boost in reproductive effort late in life. If kittiwakes have some method of tracking their reproductive performance, then it is possible that individuals that experienced early failures might respond by taking on similar added risk in an attempt to boost their lifetime reproductive success. In support of this idea, Sullivan (2004) showed that manipulated birds from this study population changed nest sites more often than their non-manipulated counterparts, despite the potential risks associated with this behavior

(see Bried & Jouventin 2002). In the current study, we cannot determine whether the lower rate of non-breeding among the manipulated birds was the result of increased reproductive effort on their part, or simply due to a long-term cost of early breeding being expressed in the non-manipulated population. It is also possible that both mechanisms may have contributed. Breeder abundance and productivity declined at the colony during the late 2000s, so it is unlikely that environmental conditions contributed to increased breeding effort in the later years of the study. In any case, disentangling these alternative hypotheses poses an interesting challenge for future research.

CONCLUSIONS

Reproductive costs in long-lived taxa may persist well beyond the current breeding season, and these persistent costs may be preferentially shunted toward less critical demographic parameters in favor of maintaining survival. We observed an apparent reproductive cost in the form of reduced future breeding propensity, despite seabirds' well-known capacity to buffer reproduction via behavioral plasticity (e.g., Grémillet *et al.* 2012; Harding *et al.* 2013). In contrast, we observed no effect on long-term survival probabilities, suggesting that survival is particularly resistant to change. Such resistance implies that declining adult survival rates in a monitored seabird population may indicate exhausted buffering capacity. In this event, management strategies aiming to reduce breeding costs may allow reproductive cost savings that enhance long-term survival, a critical demographic parameter to the persistence of long-lived populations.

ACKNOWLEDGMENTS

For field assistance, we would like to thank Andrew Allyn, Emily Bernhardt, Karen Brenneman, Traci Caddy, Dan Cushing, Chelsea Effinger, Max Kaufman, Laura Kennedy, Liz Labunski, Jeremy O'Donnell, Rebecca Pond, Alex Robbins, Ravel Sandberg-Diment, Tanya Sandberg-Diment, Ana Santos, Peter Goldberg, Kelsey Sullivan, Patti Sullivan, Gloria Zager, and Tamara Zeller. Funding for the original experiment was provided by the U.S. Fish and Wildlife Service, a grant awarded to G. Golet by the Biology Department at the University of California, Santa Cruz, and the *Exxon Valdez* Oil Spill (EVOS) Trustee Council. Funding for post-experimental re-sighting was provided by the U.S. Fish and Wildlife Service (USFWS) and the Earthwatch Institute; at the time of this publication, the data have not been published by USFWS. Administrative, financial, and computer support during data analysis and manuscript development was provided by the University of Maine through the Cooperative Agreement with the U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit. This study does not necessarily reflect the views of the EVOS Trustee Council, the Earthwatch Institute, or the U.S. Fish and Wildlife Service. Mention of trade names and commercial products does not constitute endorsement or recommendation for use by the U.S. Government.

CHAPTER 5: SURVIVAL AND RECRUITMENT DYNAMICS OF BLACK-LEGGED KITTIWAKES *(RISSA TRIDACTYLA)* FROM AN ALASKAN COLONY

ABSTRACT

The majority of seabirds breed colonially and exhibit considerable site fidelity over the course of their long lifespans. Initial colony selection can therefore have substantial fitness consequences, but factors contributing to recruitment into colonies and subsequent fidelity remain unclear. We used multi-state capture-recapture models to test several hypotheses related to apparent fledgling survival, the probability of recruitment to natal colonies, and apparent post-recruitment survival in Black-legged Kittiwakes using data from individuals banded as chicks and subsequently resighted at a colony in south-central Alaska over a twenty-year period. Competitive models suggested that apparent fledgling survival declined throughout our study; this decline was likely driven by intrinsic, cohort-specific processes and was not explainable by post-fledging wind and climate conditions. Independent resighting efforts at other colonies suggest the apparent decline may have been at least partially influenced by permanent emigration (natal dispersal) that occurred more frequently during later study years. Recruitment was primarily age-dependent, with no detectable effect of early life experience or annual changes in colony size, colony productivity, climate, or average weather conditions. We estimated an average recruitment age of seven years, which is older than typically reported for Atlantic kittiwake populations, and supports a more conservative life history strategy for kittiwakes in the Pacific. Variation in apparent survival of recruits was

cohort-specific and did not correlate with age or annual changes in the factors listed above. Instead, apparent survival of recruits was best explained by colony size during a cohort's second year, suggesting a degree of negative density dependence in post-recruitment fidelity. This information could prove useful to managers deciding how to allocate resources among small, growing colonies and large, well-established colonies.

INTRODUCTION

Colonial breeding is nearly ubiquitous among seabirds (Coulson 2001). The behavior may provide an informational advantage for birds foraging in a patchy and unpredictable environment (Clode 1993, Buckley 1997, but see Rolland *et al.* 1998), but any such advantage comes at a cost which may be proportional to the size of the colony. Dense colonies can attract seabird predators (Coulson 2002, but see Hernandez-Matias *et al.* 2003) that can have substantial influence on nest site choice (Martin 1995, Eggers *et al.* 2006) and breeding success (e.g. Regehr & Montevecchi 1997, Wittham & Leonard 1999). Coloniality can also increase intraspecific competition (Tella *et al.* 2001), risk of ectoparasitism (Moller 1987, Mangin *et al.* 2003), and pathogen transmission (Clancy *et al.* 2006).

Patterns of colony recruitment and fidelity likely reflect life history strategies. The age of recruitment greatly influences lifetime reproductive success (Stearns 1992) but is subject to significant tradeoffs with future reproductive potential (e.g., Reed *et al.* 2008, *but see* Aubry *et al.* 2011). These tradeoffs may favor different strategies in populations under different constraints, leading to different recruitment patterns. Fitness tradeoffs may also determine fidelity to particular colonies or nest sites following recruitment;

there is some relationship between life expectancy and fidelity for some seabird taxa (Bried & Jouventin 2002). This relationship suggests that a longer lifespan is associated with a "stay and tolerate occasional costs" strategy, whereas a shorter lifespan is linked to greater variability in breeding site choices from year to year. Colony quality (i.e., the probability of reproductive success for a typical colony member) can be quite variable, depending on factors such as local foraging ground characteristics (e.g., Renner et al. 2012, Paredes et al. 2012) and the degree of inter-colony competition (Cairns 1989, Ainley et al. 2003, Gremillet et al. 2004), so breeding colony choice and subsequent fidelity represent high-stakes decisions for individual birds.

In turn, events occurring at colonies undoubtedly influence population dynamics. Nest site availability at colonies may limit the number of breeders in a population (e.g., Porter & Coulson 1987). Further, species like the Red-legged Kittiwake (*Rissa brevirostris*) nest in so few or such large colonies that a single breeding site can contain the majority of the global breeding population (Byrd & Williams 1993). In these cases, colony success can drive larger population dynamics. Dispersal among colonies could also potentially influence regional population dynamics both through direct effects on production as well as alterations to genotype distribution and abundance patterns.

Intrinsic processes clearly play a regulatory role within seabird colonies. Density dependent relationships between colony size and reproductive success are well-documented (e.g., Hunt *et al.* 1986). Such relationships stem at least partially from localized prey depletion (e.g., Lewis *et al.* 2001, Forero *et al.* 2002), which forces birds nesting in large colonies to forage farther from the colony (Ainley *et al.* 2003, Grémillet *et al.* 2004), presumably at greater cost. Density dependence can also influence

recruitment (e.g., Crespin *et al.* 2006). The role of density dependence in fidelity patterns, however, remains somewhat more enigmatic. In Black-legged Kittiwakes *(Rissa tridactyla,* "kittiwake" hereafter), breeding patch success rather than breeder density is the dominant consideration in movement decisions (Danchin *et al.* 1998). Although new, small colonies can be more productive than large, established colonies, birds may be reluctant to form new colonies (Kildaw *et al.* 2005), suggesting hidden costs associated with new colony formation, or, alternatively, that strong fidelity may sometimes represent an evolutionary trap. We know even less about how extrinsic processes shape colony dynamics, though seabird recruitment patterns have been tied to climate patterns (Crespin *et al.* 2006) and predator density (Finney *et al.* 2003)

Our goal in this work was to explore return and recruitment dynamics of seabird colonies. We focus on three questions: (1) What factors contribute to the return of fledglings to their natal colony? (2) What influences their recruitment to these colonies and, (3) once recruited, what factors contribute to their continued return? We approached these questions with a suite of specific hypotheses related to apparent fledgling survival, recruitment, and apparent recruit survival (Table 5.1) of Black-legged Kittiwakes *(Rissa tridactyla,* "kittiwake" hereafter) at a south-central Alaskan colony. We tested these hypotheses using multi-state capture-mark-recapture (CMR) modeling. Our objectives were to determine whether intrinsic or extrinsic processes drive these vital rates and to evaluate evidence for a more conservative life history strategy in Pacific vs. Atlantic kittiwakes.

METHODS

Focal species

The Black-legged Kittiwake provides an ideal case study to investigate questions regarding natal colony recruitment and fidelity and as such has contributed to numerous studies on coloniality in marine birds (e.g., Cadiou *et al.* 1999, Ainley *et al.* 2003, Kildaw *et al.* 2005, Coulson & Coulson 2008). The kittiwake is a small, long-lived, piscivorous gull with a northern circumpolar distribution and a global population size between 17 and 18 million individuals (Delany & Scott 2006). Kittiwakes are colonial cliff-nesters, rearing one, two, or rarely three young per breeding season. As in many seabird species, parents share incubation and chick-rearing duties equally (Coulson & Wooller 1984). Both mate and nest-site fidelity are high (Coulson & Thomas 1985), facilitating long-term capture-recapture studies. Kittiwake numbers within our study region of Prince William Sound fluctuate dramatically; the breeding season population size ranged from a low of 28,000 to a high of 110,000 individuals during 1989 – 2007 (McKnight *et al.* 2008). Colony occupancy and productivity in Prince William Sound are also dynamic. Between 1985 and 2012 more than forty colonies have been monitored; during this period approximately 14 new colonies were initiated, and roughly 16 colonies were abandoned (Irons, unpublished data).

Study area

The Shoup Bay kittiwake colony is located in northeastern Prince William Sound (PWS), Alaska (61° 10’ N, 146° 35’ W; Fig. 5.1). Shoup Bay is a small fjord that adjoins the larger Port Valdez fjord with a tidewater glacier that terminates at the fjord’s western

end. The fjord connects to Port Valdez via a reversing tidal river 0.8 km in length. The kittiwake colony is located primarily on the south-facing side of a rocky island 0.4 km in length and 100 meters from the mainland. The colony was formed sometime after the colony island emerged from the receding Shoup glacier, which still covered the nesting cliffs in the early 1960s; the colony was well-established by the 1980s. Through the early 2000s, the fjord was frequently filled with large icebergs calved from the glacier, until the late 2000s, when the glacier retreated mostly onto land. Predators at the colony are predominantly avian and include bald eagles *(Haliaeetus leucocephalus),* peregrine falcons *(Falco peregrinus),* common ravens *(Corvus corax),* northwestern crows *(Corvus caurinus),* and black-billed magpies *(Pica hudsonia).* Occasional mammalian predators include American mink *(Neovison vison)* and wolverine *(Gulo gulo).*

Field data collection

CAPTURE/RESIGHT SAMPLING -- Annually during 1979 and 1988-2008, we banded 369 ± 74 (95% confidence interval) 12-32 day-old kittiwake chicks at the Shoup colony by temporarily removing them from nests by hand. We individually marked chicks with unique color band combinations. From 1992-2010, 4 to 8 observers read color bands using binoculars and 60X spotting scopes (hereafter referred to as resighting) during mornings and evenings in May when breeders were actively building nests. Major nesting sections (N=10) were delineated using cliff features, and birds were resighted within each section an average of 9.8 (± 0.35 SD) times throughout the nesting season.

We evaluated individual breeding status based on the number of times a bird was recorded at a specific nest location. Holding a nest site is the essential condition that

affects kittiwake survival irrespective of reproductive success (Aubry et al. 2011) and thus provided a reasonable representation of breeding intent in our survival models. Birds seen at a particular nest site three or more times were considered to be probable breeders ("breeders" hereafter). Birds seen fewer than three times on a single site were noted as probable non-breeders ("non-breeders" hereafter), i.e., they were present but not engaged in intensive nesting behavior. While predation was substantial during some years, the majority of predation affected nestlings and occurred after the period when we resighted marked individuals at the colony, and thus did not appreciably influence breeding status assignments by removing banded breeders prior to their third sighting.

BREEDING POPULATION SIZE AND PRODUCTIVITY -- To assess the role of intrinsic colony processes in determining vital rate patterns, we included metrics describing colony size and productivity in modeling. Beginning in 1985 and continuing through 2012, we visited the Shoup Bay kittiwake colony twice annually as part of a larger effort to document breeding effort and productivity at all kittiwake colonies in Prince William Sound. In late May/early June, when birds had begun incubation, we counted all active nests (attended by at least one bird) on all faces of the colony with binoculars from an 8m fiberglass boat floating 100-200m from the cliff faces. We returned in late July/early August each year to count chicks and fledglings using the same method at a stage of development when most chicks were large enough to be easily visible in the nests. We also included several measures of prey availability: herring spawn activity within foraging range (40 km) of the colony (Moffit 2016; see Chapter 1 for

details), and modeled age-1 abundance for the Prince William Sound region (HRMT 2014).

ENVIRONMENTAL VARIABLES -- In addition to breeding kittiwake metrics described above, we also considered a number of extrinsic factors in modeling that might affect kittiwake survival and recruitment. We suspected that winter conditions were important, but given Shoup kittiwakes' diverse migratory strategies, choosing a single metric to represent winter posed a challenge. Because kittiwakes apparently migrate in some years but remain in the northern Gulf of Alaska in others (McKnight et al. 2011), we hypothesized that birds may face a tradeoff between costs associated with migration and constraints of reduced winter day lengths in the high latitudes. Migratory decisions therefore might be made based on local conditions affecting forage efficiency, specifically wind and sea surface temperature. We therefore used several metrics to represent both winter and spring weather conditions on the northern coastal shelf of the Gulf of Alaska. First, we calculated the mean winter (November through February) Pacific Decadal Oscillation index value, which is based on the first principal component of North Pacific (> 20° north latitude) monthly sea surface temperature anomalies (JISAO 2016). We similarly computed the mean winter El Niño – Southern Oscillation (ENSO) index value based on a five month running mean of sea surface temperature anomalies in the region between 5°N-5°S and 170°W- 120°W (ESRL 2016a). For an index of fall (September through October), winter, and spring (March through April) weather conditions in the northern coastal shelf of the Gulf of Alaska, we extracted the monthly modeled wind magnitudes for 59°N 147°W *(*ESRL 2016b), and used the average

value for each period. We also averaged monthly sea surface temperatures for the same region of the Gulf of Alaska from the National Oceanic and Atmospheric Administration's optimally interpolated sea surface temperature data (ESRL 2016c). We used Z-standardization to center and scale all continuous covariates prior to modeling.

Data analysis

MULTI-STATE MODELING -- We used multi-state models (Nichols & Kendall 1995) to test hypotheses about factors governing apparent fledgling survival, recruitment, and apparent recruit survival (Table 5.1) in kittiwakes. Multi-state modeling allowed us to simultaneously estimate resighting probability (p), the probability of transitioning between pre-defined states (ψ), and apparent survival probability (ϕ). We acknowledged that this population was not completely closed and permanent emigration was possible during our study. Thus we interpret survival estimates as apparent survival, which reflects a combination of true mortality and permanent emigration from the study colony (i.e., true survival is likely underestimated).

We conducted our analyses in three stages to determine the most parsimonious model structure for p, ψ, and φ. In the first stage, we evaluated a set of resighting probability models while allowing a fully general model structure for survival and transition probabilities. During the second stage of analysis, we applied the best resighting structure to a candidate set of transition models with fully state- and time-dependent survival structure to test hypotheses regarding transition probabilities. Finally, in stage three, we used the best resighting and transition probability structures to build candidate models representing hypotheses addressing apparent survival.

Within this general framework, we used a two-phase approach within each stage of the analysis to evaluate fundamentally different sources of variation in each vital rate. During phase I, we evaluated general sources of variation for each parameter (p, ψ, φ) by fitting five alternative models: constant (intercept only), year (as a fixed effect), age (or age class), cohort (determined by hatch year), and breeding state, along with any additive and interactive combinations of these factors appropriate to the parameter. We further considered that year, cohort, and age effects may interact with breeding state, and that year and cohort may interact with life stage (juvenile vs. adult; "age class" hereafter). For phase II, we used the best-supported model structure from phase I, but substituted explanatory covariates consistent with our sub-hypotheses associated with the best supported structure (Table 1) for the more general model components that were supported in phase I. For example, if year was supported as a fixed effect in the first phase of hypothesis testing, then during phase II we considered covariates that varied annually (e.g., colony size) and could provide a biological mechanism for the annual variation supported in phase I.

We performed all demographic modeling using the RMark package (Laake 2013) in Program R (R Core Team 2016) to interface with Program MARK (White & Burnham 1999). We adjusted AIC to AIC_c to account for small effective sample sizes. We assessed goodness-of-fit of the most general model (with p, ψ, and φ structures all set to full state and time dependence) using the median c-hat test in Program MARK and used the test results to calculate a variance inflation factor, adjusting AIC_c values to $QAIC_c$ for the entire model set, as appropriate. We used $QAIC_c$ model selection procedures to evaluate support for competitive models (Burnham and Anderson 1998). We considered any

model structure to be competitive if it successfully converged, if the 85% confidence intervals of beta estimates associated with the model's core hypothesis did not overlap 0.0 (Arnold 2010), and if AIC scores fell within 2.0 units of the best model from the candidate set in question. We considered a hypothesis supported over alternate hypotheses if its model Akaike weight was greater than all other models combined. For models with full annual time-varying structure in both p and ϕ or ψ, we avoided interpretation of parameter estimates for the final time period, during which survival/transition and resight probabilities are confounded in the model likelihood. We report 95% confidence intervals for real parameter estimates as the 2.5 (lower) and 97.5 (upper) percentiles of bootstrapped ranges (10,000 iterations), calculated using logit back-transformed beta coefficients.

APPARENT FLEDGLING SURVIVAL AND RECRUITMENT -- To test hypotheses regarding apparent fledgling survival and recruitment (i.e., permanent transition from the pre-breeder to the breeder state), we constructed models using data from chicks banded in 1991 and 1995 – 2006 (N = 5,090). Using 2006 as our end year ensured that all birds were at least four years of age during the final year of resighting; 90 percent of returning chicks from the 1991 – 1999 cohorts (N = 1,329) had returned at least once by age four. We assigned each bird to one of two states in every year it was detected: "pre-recruits" included chicks and any birds present but not documented as breeders in the current or previous years, whereas "recruits" included birds classified as breeding during the current or previous years. State membership was therefore not synonymous with presence. To facilitate modeling, we simulated the release of all birds as age 1 pre-recruits to eliminate

the mathematical gap between the banding year (age 0) and the earliest possible sighting (age 2) for most birds; one year-old returns were negligible (N = 8 of 5,090 individuals). Parameter estimates for the first interval therefore represented the cumulative probability of apparent survival associated with the first two years combined. Cohort-specific covariates were assigned accordingly to account for this adjustment. We assigned birds to one of two age classes in each year, juvenile (0-2 years) and adult (3 years and older), acknowledging that the transition between age classes occurred before most individuals returned to the colony for the first time. This distinction allowed us to calculate separate parameter estimates for fledglings in their first 2 years of life. To improve estimation, we fixed the following parameters to zero: the probability of transitioning from a breeder to pre-recruit, and survival and resighting probabilities for missing cohorts (i.e. years in which banding did not occur). Because 95% of all recruiting individuals were classified as breeders by age 12, we also fixed the probability of transitioning from pre-recruit to a breeder to 0.0 after age 12.

We used estimates from the best-supported model to calculate a cumulative transition probability, γ, that gave the probability a bird would recruit to the breeding population at or before age *j*, as

$$\gamma_j = \sum_{i=1}^{j} [\psi_j * \prod_{i=1}^{j-1} (1 - \psi_i)]$$

where γ returns the probability that a bird would recruit to the breeding population at or before age *j*, and the probability of recruitment at a given age was conditional on not recruiting during any prior year, and was also implicitly conditional on survival. The age

at which cumulative recruitment probability first surpasses 0.5 represents the average recruitment age, ω, of the sampled cohorts.

Finally, we assessed the probability of survival to the average recruitment age. To do this, we used the coefficients from the best supported model to calculate the cumulative probability, η, of pre-recruits surviving to the average age of recruitment, ω, for each cohort k as:

$$\eta_k = \prod_{A=0}^{\omega_k} \varphi_A$$

We then calculated the geometric mean of these cumulative probabilities over all cohorts that reached the mean recruitment age during the course of the study to approximate the mean probability of recruitment.

APPARENT SURVIVAL OF RECRUITS -- To test hypotheses regarding post-recruitment fidelity, we used resighting data from only the 1991 and 1995-2004 cohorts; members of later cohorts were less likely to have recruited by the time resighting ceased in 2010. Further, we were interested solely in factors associated with recruitment and later fidelity, so we included only those individuals that eventually recruited to the Shoup colony (N = 997) in the modeled dataset. We identified three breeding states: "pre-recruit" (as described above), "breeder" (observed three times on the same nest site), and "non-breeder" (a former breeder observed <3 times on a single nest site). To facilitate estimation, we released all individuals as two-year olds for reasons described above. Because the modeled dataset included only eventual recruits, we lost little information in eliminating records of pre-recruit returns at age two, as the number of reported age two

breeders was negligible (five of 997 individuals). Parameter estimates for the first modeled time period therefore represented cumulative probabilities across a three-year period. Once again, we assigned each bird sighting as either a juvenile or adult, as defined previously. This distinction allowed us to separate the recruitment probability of three year olds from that of older birds. As in the fledgling survival analysis, we fixed several parameters to improve model estimation: we fixed all impossible transition probabilities to zero (e.g., nonbreeder to pre-recruit), all survival probabilities of pre-recruits to 1.0, and all survival and resight probabilities for missing cohorts to zero.

Assessment of the closure assumption

Our data did not allow us to estimate permanent emigration directly; however, we conducted a cursory assessment of permanent emigration using independent resighting work from two time periods within the larger study period to provide context for apparent survival estimates. To this end, we used ancillary resighting data collected with comparable methods from other colonies within Prince William Sound in 1997 – 1999 (D. Irons, unpublished data) and from the new Valdez pipeline terminal dock colony (<10 km from the Shoup colony) in 2007 to assess the relative degree of emigration in the 1990s vs. the 2000s. We calculated the proportion of each cohort with members aged 5-11 observed nesting outside of Shoup Bay in 1997-1999 and at the pipeline terminal colony in 2007. We chose eleven years as the cutoff because annual banding began in 1988 at the Shoup Bay colony; birds in this cohort would have been age 11 in 1999. We then calculated the percentage of the pipeline terminal group that had never been detected at the Shoup Bay colony; a similar calculation was not possible for the 1997-1999 group,

as some members carried only cohort-specific marks and were not individually distinguishable from other members of their cohorts.

RESULTS

Colony size and productivity

Colony size ranged from 8,400 to 19,000 actively breeding birds. It peaked in 2002 but declined to 14,400 active breeders by 2010. Productivity varied widely during the same period from a maximum of 0.62 chicks per nest in 1996 to a minimum of 0.00 chicks per nest in 2009, with a general decline through time (Fig. 5.2).

Apparent fledgling survival and recruitment

Of chicks banded in the 1991 and 1995 – 2006 cohorts, 35 ± 6% (mean ± 95% confidence interval) of each cohort was documented at least once at the Shoup Bay colony in the years following fledging, and 20 ± 6% of the 1991 and 1995 – 2004 cohorts (at least age 6 during the last year of resighting) were detected breeding at their natal colony.

Apparent fledgling survival appeared to be driven by factors shared among members of a cohort. After we adjusted all AIC_c to $QAIC_c$ with the estimated variance inflation factor $\hat{c} = 2.13$, the best supported model structure for resighting probability included additive effects of breeding state and age class ($w_i > 0.99$; Table D1) and the best performing model structure for transition probability contained only an age effect ($w_i > 0.99$; Table 5.2). The top ranked general model of apparent fledgling survival included an interaction between age class and cohort ($w_i > 0.99$; Table D2, Fig. 5.3); indicating that

apparent fledgling survival is influenced by events that affect cohorts independently (e.g., events occurring during a sensitive age or immediately after the hatch year). Hypotheses involving time-varying factors were not supported; apparent fledgling survival was not closely linked to annual variations in colony characteristics or environmental conditions. Of the models reflecting our specific cohort-based hypotheses, the top-ranked model included a negative effect of hatch year population size (w_i >0.99; Table 5.3). However, none of the models reflecting specific cohort-based hypotheses outperformed the general cohort structure.

Resight probability was 0.53 (95% CI = 0.47-0.57) for pre-recruitment adults and 0.81 (0.77-0.83) for post-recruitment adults, whereas resight probability for juveniles was 0.09 (0.08-0.10) for pre-recruits and 0.27 (0.24-0.29) for two year-old breeders. Probability of recruitment peaked between ages five and six at 0.21 (0.17-0.25), then declined until age 10, when the cumulative probability of recruitment had reached 0.69 (Fig. 4). Average recruitment age was seven years. Apparent survival of fledglings generally declined over cohorts from a peak of 0.81 (0.73-0.87) for the 1995 cohort down to 0.23 (0.10 – 0.47) for the 2005 cohort, but once individuals reached adulthood, apparent survival was variable with no obvious trend. Cumulative probabilities of survival to age seven (average modeled recruitment age) for the 1991 and 1995 – 2003 cohorts (at least seven years of age during the final resighting effort in 2010) were 0.23 (0.17 – 0.31).

Post-recruitment fidelity

Factors shared among members of a cohort also drove post-recruitment apparent survival. After we adjusted all AIC_c to $QAIC_c$ based on a variance inflation factor of $\hat{c}$ = 1.76, the best supported model structure for resighting probability included additive effects of breeding state and time ($w_i > 0.99$; Table D3). The best performing model structure for transition probability contained interactive effects of breeding state and year ($w_i > 0.99$; Table D4). The top ranked variability structure in apparent survival included additive effects of state and cohort ($w_i = 0.94$; Table D5), supporting our hypothesis that post-recruitment apparent survival was driven by factors shared among a cohort. The analysis did not support hypotheses that apparent survival was a function of age or temporal variation. Of the models reflecting specific cohort-based hypotheses, the top-ranked model included a term for the colony size during the cohort's second year (w_i = 0.74, Table 5.4). Models containing a population size term for the cohort's second year or third year, by which time 63% and 85%, respectively, of all individuals that eventually returned had been detected at the colony, had a combined Akaike weight of 0.99.

Pre-recruit resight probabilities were lower and more variable (0.45 - 0.80) than those of post-recruits (0.70 - 0.94). Non-breeders had higher resight probabilities than breeders, likely due to the more stringent observation criteria for breeders, though confidence intervals overlapped substantially. Juvenile transition probabilities, which ranged from 0.11 to 0.55, were higher and more variable than those of adults, which ranged from 0.02 to 0.23. The colony size at age two had a negative influence on a cohort's post-recruitment fidelity (Fig. 5).

Table 5.1. Vital rate hypotheses. Hypotheses explaining apparent fledgling survival, recruitment, and post-recruitment fidelity in Black-legged Kittiwakes from the Shoup Bay colony in Prince William Sound, Alaska, U.S.A., along with variables and their sources used in multi-state capture-recapture models representing each hypothesis.

Hypothesis	Variables	Source
Vital rate is a function of cohort-specific factors.		
	Carryover effects (fledging survival only)	
	Herring spawn activity within colony foraging range during: (1) hatch year, (2) previous breeding season (parental effect)	Moffitt 2016; see CHAPTER 4 for details
	Modeled age-1 herring abundance in PWS region during: (1) hatch year, (2) previous breeding season (parental effect)	HRMT 2014
	Early life experience	
	Colony size in cohort's hatch year	U.S. FWS monitoring data
	Colony productivity in cohort's hatch year	U.S. FWS monitoring data
	Post-fledging environmental conditions	
	Mean first winter* PDO index values	JISAO 2016
	Mean first winter Nino 3.4 index values	ESRL 2016a
	Mean monthly modeled first fall**, winter, and spring*** winds in northern GOA (58N, 147W)	ESRL 2016b
	Mean monthly first winter sea surface temperature in northern GOA (58N, 147W)	ESRL 2016c
	Prospecting experience	
	Natal colony size at cohort ages 2 or 3	U.S. FWS monitoring data
	Natal colony productivity at cohort ages 2 or 3	U.S. FWS monitoring data
Vital rate is a function of time-varying factors.		
	Natal colony size in current, previous year	U.S. FWS monitoring data
	Natal colony productivity in previous year	U.S. FWS monitoring data
	Environmental conditions in current, previous year (listed above)	JISAO, University of Washington
Vital rate is a function of age (recruitment and post-recruitment fidelity only).		U.S. FWS monitoring data
Vital rate is constant.		

* *Averaged monthly data from November through February prior to the breeding season*
** *Averaged monthly data from September and October*
*** *Averaged monthly data from March through April prior to the breeding season.*

Table 5.2. Recruitment probability model performance. Performance of competing models exploring the best general structure for multistate models estimating the probability of state transition (ψ), where states were pre- vs. post-recruitment, for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony, Prince William Sound, Alaska, during 1991-2008. Model structure for resight probability was set to the best competing structure (recruitment state + age class,), and survival was set to general state and time dependence. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. ΔQAICc values reflect ΔAICc values adjusted according to a median ĉ estimate of 2.13.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
	Recruitment probability varies ...			
$\Psi_{(age)}$	... among ages only.	0	> 0.99	51
$\Psi_{(time)}$	... among years only.	160.24	< 0.01	57
$\Psi_{(cohort)}$	... among cohorts only.	230.67	< 0.01	57
$\Psi_{(constant)}$	Recruitment probability does not vary.	293.75	< 0.01	40

Table 5.3. Fledgling survival probability model performance. Performance of competing multi-state models testing hypotheses to explain the observed cohort effect on apparent survival (φ; survival + fidelity) of Black-legged Kittiwakes banded as chicks at the Shoup Bay colony, Prince William Sound, Alaska, during 1991-2008, with the top-ranked general model (age class * cohort; itallicized) included for reference. Asterisks denote interactive models, which include both additive and interactive effects. Model structure for resight probability was set to the best competing structure (recruitment state + age class, where states were pre- vs. post-recruitment), and transition model structure was set to the best competing structure from transition modeling (age). Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. ΔQAICc values reflect ΔAICc values adjusted according to a median ĉ estimate of 2.13.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
	Apparent survival varies ...			
$\varphi_{(age\ class * cohort)}$	*... between age classes and among cohorts, with a different cohort pattern between age classes.*	*-78.47*		*41*
$\varphi_{(age\ class * HY\ pop\ size)}$	... between age classes and by hatch year colony size, with a different colony size pattern between age classes.	0	> 0.99	19
$\varphi_{(age\ class * pre\text{-}HY\ herring\ spawn)}$	... between age classes and by herring spawn activity within colony foraging range in breeding season prior to hatch, with a different herring spawn pattern between age classes (parental effect).	68.4	< 0.01	19
$\varphi_{(age\ class * HY\ herring\ spawn)}$	... between age classes and by herring spawn activity within colony foraging range during hatch season, with a different herring spawn pattern between age classes.	68.4	< 0.01	19
$\varphi_{(age\ class * age\ 2\ pop\ size)}$	... between age classes and by colony size during the cohort's second year, with a different colony size pattern between age classes.	73.12	< 0.01	19
$\varphi_{(age\ class * HY\ age\ 1\ herring)}$	... between age classes and by PWS modeled age 1 herring abundance in hatch year, with a different herring pattern between age classes (parental effect).	79.75	< 0.01	19
$\varphi_{(age\ class * pre\text{-}HY\ age\ 1\ herring)}$	... between age classes and by PWS modeled age 1 herring abundance in breeding season prior to hatch, with a different herring pattern between age classes (parental effect).	79.76	< 0.01	19
$\varphi_{(age\ class * age\ 3\ pop\ size)}$	... between age classes and by colony size during the cohort's third year, with a different colony size pattern between age classes.	87.7	< 0.01	19
$\varphi_{(age\ class * age\ 3\ prod)}$	... between age classes and by colony productivity during the cohort's third year, with a different productivity pattern between age classes.	98.22	< 0.01	19
$\varphi_{(age\ class * AHY\ spring\ winds)}$	... between age classes and average spring winds in the northern GOA following the cohort's first winter, with a different wind pattern between age classes.	105.08	< 0.01	19
$\varphi_{(age\ class * HY\ prod)}$	... between age classes and by colony productivity during the cohort's hatch year, with a different productivity pattern between age classes.	115.61	< 0.01	19
$\varphi_{(age\ class * first\ winter\ winds)}$	... between age classes and by average hatch year winter winds in the northern GOA, with a different wind pattern between age classes.	126.79	< 0.01	19
$\varphi_{(age\ class * AHY\ PDO)}$	... between age classes and by the PDO value from the cohort's first winter, with a different PDO pattern between age classes.	128.37	< 0.01	19
$\varphi_{(age\ class * age\ 2\ prod)}$	... between age classes and by colony productivity during the cohort's second year, with a different productivity pattern between age classes.	129.63	< 0.01	19
$\varphi_{(age\ class * HY\ PDO)}$	... between age classes and by the PDO value from the winter prior to the cohort's hatch, with a different PDO pattern between age classes.	133.52	< 0.01	19
$\varphi_{(age\ class * HY\ fall\ winds)}$	... between age classes and by average hatch year fall winds in the northern GOA, with a different wind pattern between age classes.	134.11	< 0.01	19
$\varphi_{(age\ class * first\ winter\ SST)}$	... between age classes and by average hatch year winter SST in the northern GOA, with a different SST pattern between age classes.	136.9	< 0.01	19

Table 5.4. Recruit survival probability model performance. Performance of competing multi-state models testing hypotheses to explain the observed cohort effect on apparent survival (φ; survival + fidelity) of post-recruitment breeders and non-breeders (determined by nest-site attendance) for Black-legged Kittiwakes banded as chicks at and eventually recruiting to the Shoup Bay colony, Prince William Sound, Alaska, during 1991-2006, with the top-ranked general model (breeding state + cohort; itallicized) included for reference. Asterisks denote interactive models, which include both additive and interactive effects. Model structures for resight and transition probability were set to the best competing structures (state + time and state * time, respectively). Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
	Survival probability of recruits varies ...			
$\varphi_{(state + 2Y\ pop\ size)}$	... between breeding states and by colony size in a cohort's second year.	0.00	0.74	73
$\varphi_{(state + 3Y\ pop\ size)}$	... between breeding states and by colony size in a cohort's third year.	2.42	0.22	73
$\varphi_{(state + HY\ pop\ size)}$	... between breeding states and by colony size in a cohort's hatch year.	6.69	0.03	73
$\varphi_{(state + cohort)}$	*... between breeding states and among cohorts.*	*8.74*	*0.01*	*82*
$\varphi_{(state + HY\ PDO)}$	... between breeding states and by winter PDO value prior to a cohort's hatch year.	14.67	<0.01	73
$\varphi_{(state + AHY\ PDO)}$	... between breeding states and by winter PDO value in a cohort's hatch year.	15.96	<0.01	73
$\varphi_{(state + HY\ Prod)}$	... between breeding states and by colony productivity in a cohort's hatch year.	16.96	<0.01	73
$\varphi_{(state + 3Y\ Prod)}$	... between breeding states and by colony productivity in a cohort's third year.	17.01	<0.01	73
$\varphi_{(state + 2Y\ Prod)}$	... between breeding states and by colony productivity in a cohort's second year.	17.29	<0.01	73

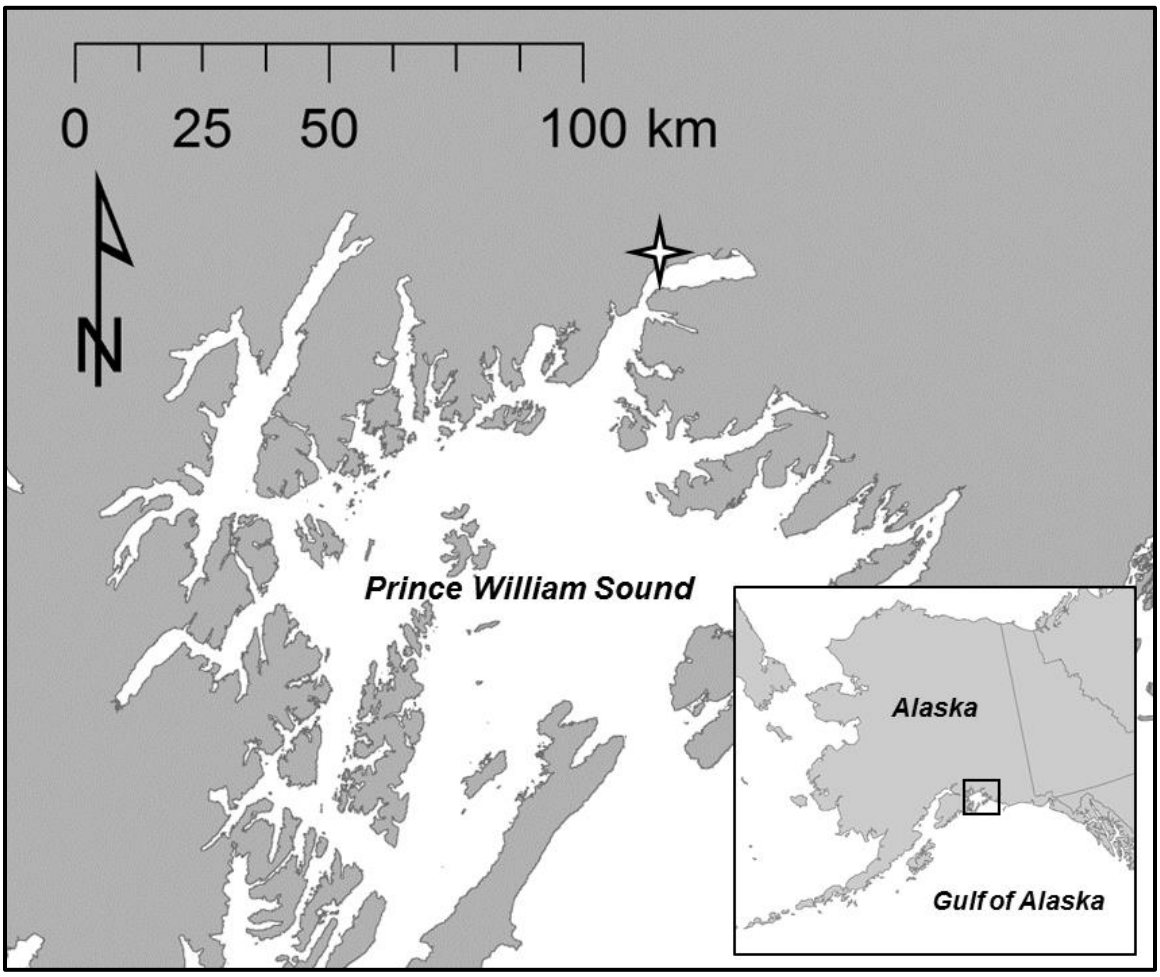

Figure 5.1. Study site location. Location (indicated by star) of the Shoup Bay kittiwake colony in Prince William Sound, Alaska. Inset map shows the location of Prince William Sound within Alaska.

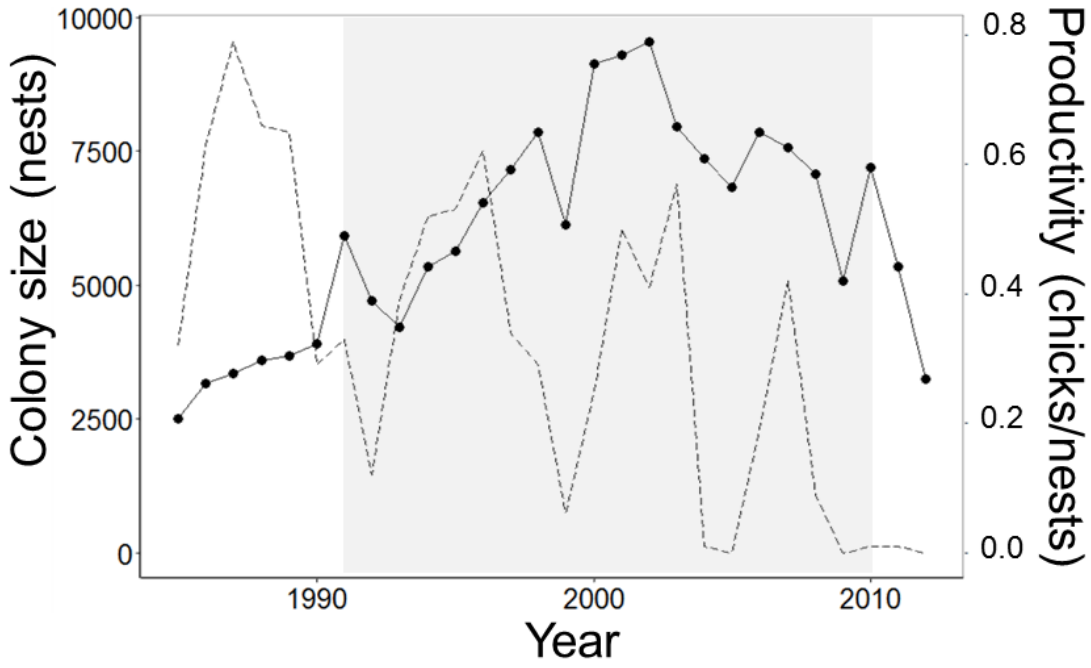

Figure 5.2. Colony size and productivity over time. Total nests (left axis; solid line) and productivity measured as total chicks divided by total nests (right axis; dotted line) of the Shoup Bay kittiwake colony in Prince William Sound, Alaska from 1985 - 2012. Gray box denotes the time period assessed in the present study (1991 – 2010). (D. Irons, unpublished data).

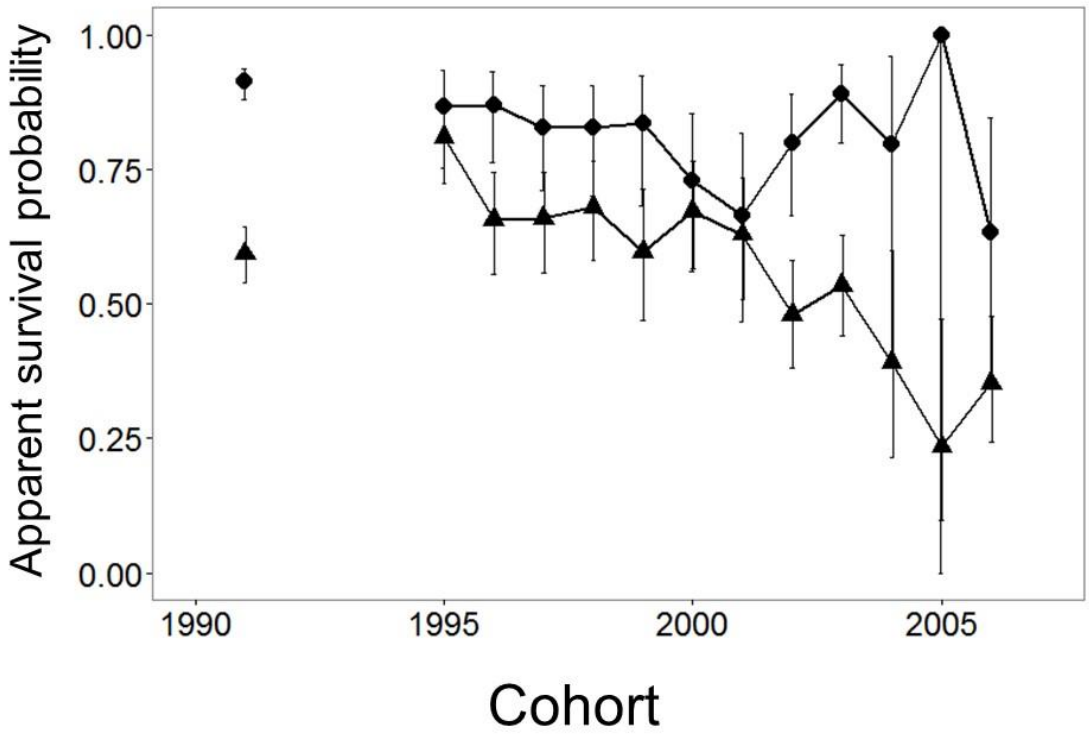

Figure 5.3. Fledgling and adult survival. Apparent survival probabilities (φ; survival + fidelity) of juveniles (age 0 – 2; triangles) and adults (age 3+; circles) by cohort from the top-ranked survival model (φ ~ age class * cohort, p ~ breeding state + age class, ψ ~ age) for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony in PWS, AK in 1991 and 1995-2006. Error bars denote the 2.5 and 97.5 percentiles of bootstrapped estimate distributions (10,000 iterations).

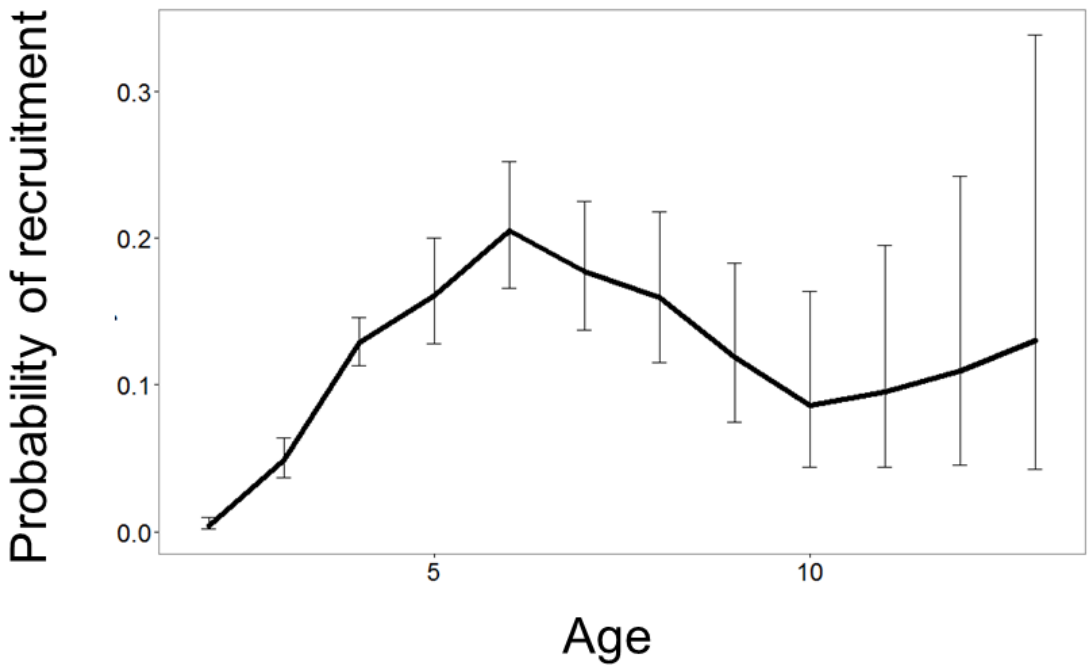

Figure 5.4. Age-based recruitment probability. Recruitment probabilities from the top-ranked model of fledgling return rate (φ ~ age class * cohort, p ~ breeding state + age class, ψ ~ age) for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony in PWS, AK in 1991 and 1995-2006. Error bars denote the 2.5 and 97.5 percentiles of bootstrapped estimate distributions (10,000 iterations).

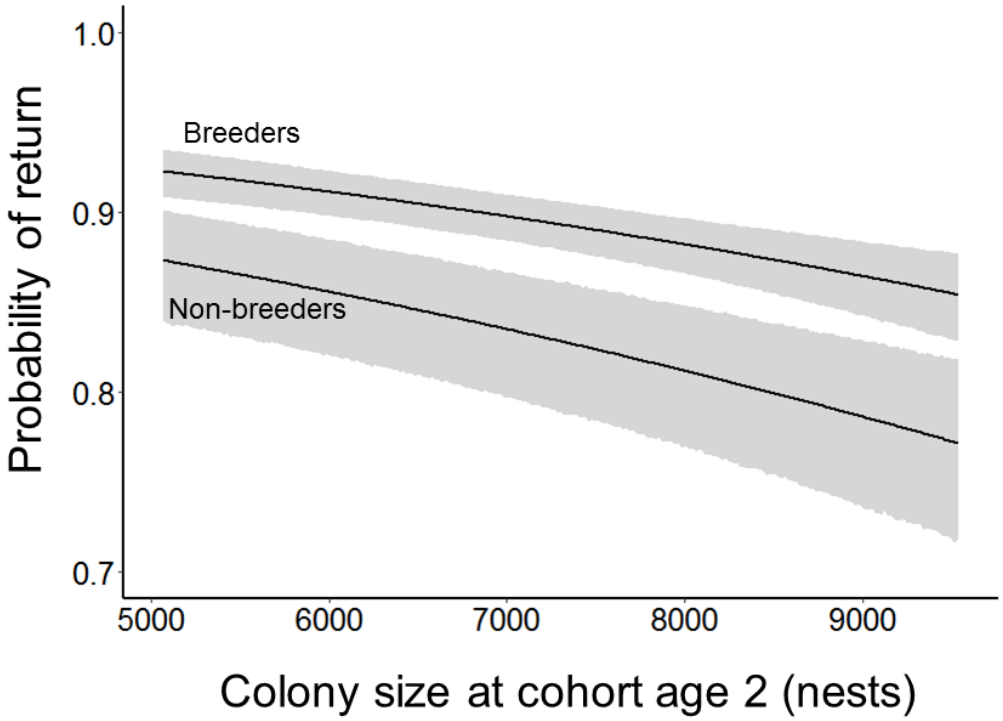

Figure 5.5. Colony size and recruit survival. Effect of natal colony size on the apparent survival of recruits from the top-ranked multi-state model explaining recruit fidelity to the natal colony as a function of natal colony size at age two in Black-legged Kittiwakes banded as chicks at and eventually recruiting to the Shoup Bay colony in PWS, AK. Breeders and post-recruitment non-breeders are denoted by the solid black lines; the gray shading denote the 2.5 and 97.5 percentiles of bootstrapped estimate distributions (10,000 iterations).

Emigration assessment

At least some part of the decline in apparent survival at the Shoup Bay colony was likely due to dispersal, which appears to have increased since the 1990s and includes established breeders. Only 1.6 ± 1.5% (95% CI) of the chicks banded in the 1988-1994 Shoup Bay colony cohorts were detected nesting at any other colony in PWS during 1997-1999. In contrast, our single visit to the Valdez pipeline terminal colony in 2007 revealed that at least 3.1 ± 0.7% of the 1996 – 2003 Shoup cohorts had established nests at that colony. Further, 38% of these nesters had never been resighted at the Shoup colony following banding, whereas 11% had previously bred at the Shoup colony; the remainder had been observed roosting at the Shoup colony.

DISCUSSION

Trends in apparent fledgling survival: evidence for increased dispersal over time

Estimating post-fledgling survival rates is challenging because of kittiwakes' tendency to remain at sea for the first two years of life and their propensity for dispersal from the natal colony (e.g., Coulson & Coulson 2008). Coulson and Ouellet (1988) estimated an overall survival rate of 0.34 from fledgling until recruitment for individuals at a well-studied British colony; Porter and Coulson (1987) reported that 11% of each cohort returned to breed at the same colony. Our cumulative probability of survival (0.23) through the average age of recruitment was somewhat lower than that of Coulson and Ouellett (1988); this difference likely reflected the younger recruitment age in Atlantic kittiwakes (4.5 years: Coulson 1966; Link, Cooch & Cam 2002; Wooler & Coulson 1977) compared to birds in our study.

Boulinier & Danchin (1997) proposed that when the environment is patchy, but site quality is stable and predictable, the optimal strategies are to (1) prospect before choosing to recruit to a site and (2) then retain or abandon sites based on the patch's rather than the individual's breeding success. When quality is predictable, higher quality colonies or patches likely attract recruits through conspecific attraction (e.g., Oro & Ruxton 2001), performance-based conspecific attraction (Danchin *et al.* 1998), or natal philopatry (where young birds recruit to the colony from which they themselves hatched, implying it was of reasonably good quality). Varying degrees of natal philopatry have been observed in many colonial birds (e.g., Thibault 1993, Aebischer 1995, Pyk *et al.* 2013, *but see* Coulson & Coulson 2008). One contributing factor appears to be the age of the colony; growth is dependent on immigration alone during the initial years of colony development until the first generations of chicks produced at the colony have reached maturity (e.g., Pyk *et al.* 2013). Following this phase, colony growth is contingent upon some combination of natal philopatry and immigration.

Crespin *et al.* (2006) found a suggestion of negative density dependence in Common Murre *(Uria aalge)* return rates that may indicate a reduction in natal philopatry at large colonies. We found a similar suggestion in kittiwakes at the Shoup colony; hatch year colony size was the best predictor of apparent fledgling survival after the general cohort-varying model structure. As colony size increases, new recruits may not have access to the best patches. Such limitation is likely responsible for slower growth in large colonies compared to small colonies (e.g., Porter & Coulson 1987, Chapdelaine & Brousseau 1989). In large colonies, dispersal away from the natal colony may then become the better strategy over philopatry. Steiner & Gaston (2005) documented greater reproductive

success in Thick-billed Murres (*Uria lomvia*) that dispersed from their natal colony, presumably owing to a greater choice in sites and mates.

Such strategic dispersal likely contributed to the apparent decline in apparent survival of fledglings that we observed at the Shoup Bay colony. Recruits from Shoup were very rare at other PWS colonies in the late 1990s but were more numerous during a survey at a single neighboring colony in 2007, suggesting an increase in dispersal from Shoup over that time period. Such a decline in natal philopatry could have further reduced recruitment to the Shoup Bay colony through negative feedback on immigrants. The number of non-breeders, including pre-recruits, attending a seabird colony can be a relatively good indicator of the colony's quality (Klomp & Furness 1990, Cadiou 1999); such non-breeders may contribute to a population's resilience by filling nest sites left vacant during periods of high adult mortality (Porter & Coulson 1987). The presence of natal pre-recruits at a colony would be an even better indicator of a colony's quality than the presence of late-stage chicks, because chicks have some ability to buffer the effects of low food quality temporarily (Dahdul & Horn 2003) but may suffer greater post-fledging mortality than well-fed counterparts. Szostek *et al.* (2014) found that Common Tern (*Sterna hirundo*) immigrants were attracted strongly by local recruits and pre-recruits at the colony. If such attraction also occurs in kittiwakes, then declining numbers of pre-recruits at the Shoup Bay colony could have had a negative effect on colony growth disproportionate to their actual numbers.

Pacific vs. Atlantic life history differences

Kittiwake life history strategies differ between the two ocean basins, where Atlantic kittiwakes enjoy greater productivity compared to Pacific counterparts (Hatch *et al.* 1993) and exhibit reduced adult survival (Atlantic: Aebischer & Coulson 1990, Coulson & Thomas 1985, Coulson & Wooller 1984, Oro & Furness 2002; Pacific: Golet *et al.* 2004; Hatch *et al.* 1993). The recruitment age we estimated for Shoup Bay kittiwakes provides more evidence of this strategic difference. We estimated that individuals were on average seven years old upon recruitment to the Shoup colony; this estimate agrees with the maturation age of seven years estimated using a different method for kittiwakes at a nearby (200 km) Gulf of Alaska colony located near the continental shelf break (Vincenzi *et al.*2013). Together, these estimates stand in sharp contrast to a much younger maturation age of four to five years observed in Atlantic kittiwakes (Coulson 1966; Link *et al.* 2002; Wooller & Coulson 1977).

Gill & Hatch (2002) proposed that the differences between the two populations may be driven by differences in food availability rather than local adaptation. However, several lines of evidence suggest that food is not as limiting within Prince William Sound as it may be elsewhere in Alaska. Kittiwake colonies within 10 km of the Shoup colony that were geographically restricted to the same general foraging area grew and produced chicks during the Shoup colony's decline (chapter 1), suggesting that food limitation was not the proximate cause of decline. Instead, predation may have a greater influence on productivity in this region (chapters 1 & 2) in comparison to oceanic colonies such as the Pribilof Islands in the Bering Sea (Irons, unpublished data), where predation is minimal (Byrd *et al.* 2008) and where food is likely more limiting (e.g., Harding *et al.* 2013). The

fact that our recruitment age agreed closely with that of a Gulf of Alaska colony experiencing different prey and predator dynamics, combined with the contrast between Alaskan and western Atlantic kittiwake recruitment ages, may reflect a true phenotypic difference in life history strategy between Pacific and Atlantic populations.

Density dependence in apparent survival of recruits

We have long been aware of the role of negative density dependence in population regulation (e.g., Hassel 1975). In seabirds, this dependence is evident in the negative relationship between colony size and reproductive success (e.g., Hunt *et al.* 1986), which at least partially reflects a direct cost of large colony size in the form of localized prey depletion (e.g., Lewis *et al.* 2001, Forero *et al.* 2002). Nest site limitation can also dampen population growth potential when poorer sites (i.e., that produce few fledglings) are used at high population densities (Kokko *et al.* 2004). In this work, we have revealed another expression of negative density dependence: apparent survival of recruits was poorer when natal colony size was large early in life (Figure 5). This reduction was likely due in part to increased dispersal of established breeders when the colony was largest, as suggested by the larger numbers of Shoup emigrants detected in 2007 compared to the late 1990s.

Many species exhibit high site fidelity following recruitment (e.g., Atwood & Massey 1988, Coulson & Nève de Mévergnies 1992, Pyle et al. 2001, Kokko et al. 2004) with few established breeders switching colonies (e.g., Aebischer 1995). Emigration is not well understood but may occur more regularly when a colony is declining (e.g., Martinez-Abrain *et al.* 2003), producing few chicks (e.g., Danchin & Monnat 1992) or

experiencing a series of cumulative disturbances (Fernandez-Chacon et al 2013). Once dispersal begins, emigration can accelerate rapidly, suggesting that declining attendance may trigger other breeders to leave as well (Martinez-Abrain et al. 2003).

Nest site limitation may have contributed to emigration of recruited breeders in our work. If young recruits tend to establish nest sites on the periphery of the colony, sites established when the colony is small may become centrally located as the colony grows around them. Centrally-located nests tend to have greater quality (e.g., safety from predators) than nests at the periphery (Hamilton 1971, Vine 1971, Wittenburger & Hunt Jr. 1985, Kharitonov & Siegel-Causey 1988, *but see* Descamps et al. 2009, Minias et al. 2012). Therefore, young individuals recruiting when the Shoup colony was small may have eventually possessed higher quality nest sites than individuals recruiting when the colony was large; greater success in these higher quality patches, in turn, may have led to greater fidelity (e.g. Danchin *et al.* 1998).

Dispersal of established breeders is fairly uncommon among kittiwakes (e.g., Coulson & Nève de Mévergnies 1992); our relatively large apparent survival estimates for recruits (>0.75) support this theme. When established breeders do disperse, they tend to recruit to other existing colonies. Kildaw *et al.* (2005) documented a "threshold of reluctance" to establish new colonies, even though new colonies can be highly productive. Dispersal to new sites may simply present too many risks for the average breeder; new sites have predator dynamics, long-term food availability, and microclimate effects that are all unknown, whereas existing colonies provide copious information to potential recruits regarding food abundance and nest safety (Forbes & Kaiser 1994). However, declining productivity at the Shoup colony in the later years of our study may

have signaled to breeders that patch quality was becoming less predictable, favoring employment of the "dispersal following patch failure" strategy (Boulinier & Danchin 1997). Dispersal of breeders may have become more feasible after the establishment of nearby (<10 km) colonies in Port Valdez beginning in the late 1990s and was likely exacerbated by declining habitat quality at the Shoup colony due to post-glacial successional changes in vegetation that may have benefited predators. Because any birds nesting within Port Valdez must travel into Valdez Arm and its associated fjords to forage, we suspect that foraging grounds overlap (but see Ainley *et al.* 2003), making a move more feasible for birds already familiar with feeding conditions in the area.

Management implications

Given the recent and dramatic declines in seabird populations around the globe (Paleczny et al. 2015), understanding recruitment and emigration patterns is important not only for successful population management but also for the effective use of seabirds as ecosystem indicators (e.g., Cairns 1987, Piatt *et al.* 2007). In this work, we identified that intrinsic processes may drive apparent survival in fledglings and recruits at an Alaska seabird colony, and that declines in apparent survival likely reflect increased dispersal at larger colony sizes. This fidelity/colony size relationship could be a useful consideration for managers, as small, growing colonies may represent a more productive long-term investment than large, established colonies. Additionally, our results allowed us to estimate the average age of first reproduction for this population. The estimate agreed with that calculated for another Pacific colony, and both were several years older than recruitment ages calculated for Atlantic populations, thus strengthening the argument that

Pacific kittiwakes follow a more conservative life history strategy than Atlantic counterparts. This conservative strategy may confer added resilience to increased short-term perturbations associated with ecosystem change.

ACKNOWLEDGMENTS

For field assistance, we would like to thank Joe Albanese, Andrew Allyn, Emily Bernhardt, Karen Brenneman, Traci Caddy, Chelsea Effinger, Greg Golet, Max Kaufman, Laura Kennedy, Alex Robbins, Tanya Sandberg-Diment, Kelsey Sullivan, and Gloria Zager and the many field volunteers that made this work possible. Funding for the original experiment was provided by the U.S. Fish and Wildlife Service, the *Exxon Valdez* Oil Spill (EVOS) Trustee Council, and the Earthwatch Institute. The U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit and the University of Maine provided administrative, financial, and computer resources support during data analysis and manuscript development. This study does not necessarily reflect the views of the EVOS Trustee Council, the Earthwatch Institute, or the U.S. Fish and Wildlife Service. Mention of trade names and commercial products does not constitute endorsement or recommendation for use by the U.S. Government.

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APPENDICES

Appendix A: Supplementary Information for Chapter 2

Table A1. PWS summary statistics. Summary statistics for data used in models of Black-legged Kittiwake colony productivity in Prince William Sound, AK. All independent variables were z-standardized prior to modeling.

Metric	Minimum	Q1	Median	Mean	Q3	Maximum
Breeding pairs per colony	1	62	214	984	1139	9298
Chicks produced per colony	0	0	2	219	77	4665
Productivity per colony (chicks/nest)	0.00	0.00	0.01	0.14	0.23	1.36
Population density within foraging range (pairs/km^2)	0.09	0.39	1.21	2.24	2.74	13.46
Coefficient of variation in brood size at fledging across colony plots	0.00	1.11	1.22	1.27	1.38	2.00
Total area of foraging range (km^2)	274.95	607.05	2,274.26	2,099.32	3,271.16	4,392.79
Total shoreline area (≤ 400m from land) within foraging range (km$^{2)}$	35.45	70.84	132.98	145.93	183.31	324.05
Ratio of shoreline to total area of foraging range	0.02	0.05	0.09	0.10	0.14	0.20
Mean depth of foraging range (meters below MHHW)	-342.67	-218.34	-166.99	-175.29	-121.86	-70.30
Median depth of foraging range (meters below MHHW)	-322.31	-242.10	-196.93	-195.58	-156.03	-69.70
Amount of shallow water ≤ 30m within foraging range (number of 0.12km raster points)	1,309	2,451	8,281	9,019	10,008	36,234
Number of June days with precipitation >0mm	3.00	11.00	13.00	13.79	16.00	29.00
Number of June days with precipitation >14mm	0.00	1.00	2.00	2.98	4.00	16.00
Total June precipitation (mm)	14.00	89.00	125.00	139.20	165.00	598.00
Number of July days with precipitation >0mm	5.00	13.00	15.50	15.98	19.00	27.00
Number of July days with precipitation >14mm	0.00	2.00	4.00	4.05	6.00	13.00
Total July precipitation (mm)	34.00	118.00	168.00	173.28	217.75	487.00
E/W July winds (m/s)	-2.23	-1.60	-1.12	-1.13	-0.72	0.66
N/S July winds (m/s)	-0.11	0.55	0.90	1.02	1.41	2.67
E/W July wind magnitude (m/s)	0.10	0.72	1.12	1.18	1.60	2.23
N/S July wind magnitude (m/s)	0.02	0.55	0.90	1.03	1.41	2.67
July wind magnitude (m/s)	0.15	1.28	1.47	1.62	2.02	3.29
May SST (°C)	6.04	7.03	7.51	7.44	7.75	9.69
Average Nino 3.4 index value for the previous winter (December - February)	-1.77	-0.87	-0.20	-0.14	0.60	2.27
April PDO index value	-1.65	-0.31	0.40	0.41	1.05	2.16
May PDO index value	-1.37	-0.30	0.48	0.55	1.46	2.18
June PDO index value	-1.47	-0.44	0.40	0.32	1.04	2.76
July PDO index value	-1.86	-0.66	0.40	0.34	1.07	2.35
Herring spawn (number of 100m spawn presence raster points within foraging range)	1.14	1.14	16.78	153.34	181.78	1,540.10
Modeled number of PWS age 1 herring from age-structure-analysis (millions of fish)	0.60	2.90	22.80	120.20	125.10	1,104.70
Number of age 1 hatchery-reared salmon parr released into the fishery subdistrict	0	24,443,668	84,462,193	114,376,526	190,774,077	424,770,590
Combined number of age 1 and 2 salmon parr released into the fishery subdistrict	474	24,639,188	87,829,844	116,611,773	193,466,448	430,281,882
Adult salmon density within forage range (fish/km^2)	602	41,703	128,787	197,447	254,516	2,687,814

Table A2. GOM summary statistics. Summary statistics for data used in models of Common Tern colony productivity in the Gulf of Maine. All independent variables were z-standardized prior to modeling.

Metric	Minimum	Q1	Median	Mean	Q3	Maximum
Breeding pairs per colony	1.00	357.20	826.50	888.90	1,269.20	2,895.00
Productivity per colony (chicks/nest)	0.01	0.71	1.06	1.05	1.32	2.31
Inter-colony competition within foraging range (pairs/km^2)	-1.49	0.39	1.20	1.73	2.90	5.80
Total area of foraging range (km^2)	603.89	767.70	827.98	867.61	985.74	1,105.24
Total shoreline area ($\leq$ 400m from land) within foraging range ($km^{2)}$	14.63	40.76	110.78	114.23	161.15	230.47
Ratio of shoreline to total area of foraging range	0.01	0.04	0.12	0.14	0.19	0.32
Mean depth of foraging range (meters below MHHW)	35.67	35.67	52.64	54.92	52.64	88.47
Median depth of foraging range (meters below MHHW)	12.59	36.43	55.95	58.72	78.81	118.93
Amount of shallow water $\leq$ 18.3m within foraging range (number of 0.025km raster points)	12,140	116,316	210,429	186,049	259,996	336,633
Number of June days with precipitation >0mm	2.92	8.57	11.40	11.08	13.28	17.99
Number of June days with precipitation >14mm	-0.17	0.76	2.63	2.65	4.49	7.29
Total June precipitation (mm)	2.23	7.87	9.45	9.65	11.62	19.13
Number of July days with precipitation >0mm	0.01	1.00	1.99	2.10	2.99	7.95
Number of July days with precipitation >14mm	28.88	66.59	108.30	118.68	160.74	266.41
Total July precipitation (mm)	14.69	56.21	87.53	96.89	123.95	280.99
E/W July winds (m/s)	0.64	1.59	1.97	1.82	2.10	2.52
N/S July winds (m/s)	1.32	1.92	2.32	2.49	3.11	3.94
E/W July wind magnitude (m/s)	0.64	1.59	1.97	1.82	2.10	2.52
N/S July wind magnitude (m/s)	1.32	1.92	2.32	2.49	3.11	3.94
July wind magnitude (m/s)	2.09	2.51	3.09	3.14	3.53	4.46
May NE wind magnitude (m/s)	0.00	0.00	0.00	0.86	1.94	3.56
June NE wind magnitude (m/s)	0.00	0.89	2.37	1.87	2.72	3.61
July NE wind magnitude (m/s)	0.00	2.48	2.94	2.76	3.53	4.46
May SST (°C)	5.94	6.62	7.03	7.11	7.67	9.17
June SST (°C)	9.14	10.47	11.01	10.98	11.60	12.84
July SST (°C)	13.86	14.64	15.23	15.33	15.97	17.19
April NAO index value	-1.31	-0.34	0.26	0.30	1.11	2.55
May NAO index value	-1.55	-0.80	-0.01	-0.25	0.20	1.61
June NAO index value	-2.25	-0.91	-0.13	-0.28	0.25	1.15
July NAO index value	-3.14	-1.34	-0.39	-0.53	0.65	1.16
April AMO index value	-0.12	0.03	0.10	0.10	0.17	0.43
May AMO index value	-0.05	0.01	0.12	0.14	0.21	0.47
June AMO index value	-0.11	0.07	0.19	0.20	0.32	0.46
July AMO index value	-0.06	0.14	0.23	0.25	0.38	0.46
Herring prey (number of individuals <140mm per tow)	0.00	0.19	1.70	22.94	6.33	2,008.00
Silver hake prey (number of individuals <140mm per tow)	-0.36	0.70	3.76	8.09	13.46	116.93
Herring and hake prey (number of individuals <140mm per tow)	-0.12	-0.12	3.87	27.66	12.85	1,996.88
Herring competitors (number of individuals >140mm per tow)	-2.09	-0.54	5.57	9.43	14.32	63.84
Silver hake competitors (number of individuals >140mm per tow)	0.02	2.90	7.05	11.30	15.72	76.50
Herring and hake competitors (number of individuals >140mm per tow)	-0.94	-0.94	6.78	14.66	22.03	146.21

Table A3. Single variable models of kittiwake reproductive success. Performance of single variable generalized linear mixed effects models explaining reproductive success of Black-legged Kittiwake colonies in Prince William Sound, AK, during 1985-2012, with year and colony as random effects. Boldface type indicates top-scoring variables from each group that were used in subsequent multi-variable modeling; foraging area and SST variables were not used due to convergence problems. Akaike weights are denoted by wi, and k represents the number of model parameters.

Group	Variable	AIC	ΔAIC (overall)	ΔAIC (within group)	w_i (within group)	deviance	k
Colony size	**Number of nests at each colony in each year**	532.71	0.00	0.00	1.00	524.71	4
Inter-colony competition	**Density of kittiwake pairs within foraging range of colony**	550.92	18.21	0.00	1.00	542.92	4
Foraging area	Ratio of shoreline area (≤400m from land) to total area within foraging range of colony	556.52	23.80	0.00	0.59	548.52	4
	Total area within foraging range of colony	557.25	24.54	0.74	0.41	549.25	4
	Total shoreline area (≤400m from land) within foraging range of colony	557.36	24.65	24.65	0.00	549.36	4
Depth	**Median depth within 45 km foraging range of colony**	553.08	20.37	0.00	0.75	545.08	4
	Mean depth within foraging range of colony	556.49	23.78	3.41	0.14	548.49	4
	Amount of shallow water within foraging range of colony	556.80	24.08	3.71	0.12	548.80	4
Fish	**Modeled number of age 1 herring (one value for region)**	554.05	21.33	0.00	0.36	546.05	4
	Number of herring spawn points within foraging range of colony in current year	554.92	22.20	0.87	0.23	548.32	4
	Number of age 1 salmon released in colony subdistrict	556.32	23.60	2.27	0.12	548.33	4
	Number of herring spawn points within foraging range of colony in previous year	556.33	23.61	2.28	0.11	548.40	4
	Number of age 1 and age 2 salmon released in colony subdistrict	556.40	23.68	2.35	0.11	546.92	4
	Salmon density within foraging range of colony	557.36	24.65	3.32	0.07	549.36	4
Precipitation	**Number of June days with precipitation > 14mm (colony-specific)**	554.79	22.07	0.00	0.26	546.79	4
	Total June precipitation (mm; colony-specific)	555.42	22.70	0.63	0.19	547.42	4
	Number of July days with precipitation > 0mm (colony-specific)	555.48	22.76	0.69	0.18	547.48	4
	Total July precipitation (mm; colony-specific)	555.71	23.00	0.92	0.16	547.71	4
	Number of July days with precipitation > 14mm (colony-specific)	556.09	23.38	1.30	0.13	548.09	4
	Number of June days with precipitation > 0mm (colony-specific)	557.13	24.42	2.35	0.08	549.13	4
Wind	**Average July N/S wind magnitude (one value for region)**	549.74	17.02	0.00	0.52	541.74	4
	Average directional July N/S wind (one value for region)	550.30	17.59	0.57	0.39	542.30	4
	Average July wind magnitude (one value for region)	554.07	21.36	4.34	0.06	546.07	4
	Average July E/W wind magnitude (one value for region)	556.89	24.17	7.15	0.01	548.89	4
	Average directional July E/W wind (one value for region)	557.24	24.53	7.51	0.01	549.24	4
SST	Modeled mean May sea surface temperature (one value for region)	556.31	23.60	0.00	1.00	548.31	4
Climate	**July Pacific Decadal Oscillation index value (one value for region)**	556.05	23.33	0.00	0.25	548.05	4
	June Pacific Decadal Oscillation index value (one value for region)	557.19	24.48	1.15	0.14	549.19	4
	May Pacific Decadal Oscillation index value (one value for region)	557.22	24.51	1.17	0.14	549.22	4
	April Pacific Decadal Oscillation index value (one value for region)	557.34	24.62	1.29	0.13	549.34	4
	Average December-February ENSO Nino 3.4 index value (one value for region)	557.35	24.64	1.30	0.13	549.35	4
Null	Intercept-only model	555.38	22.66	0.00	1.00	549.38	3

Table A4. Multiple variable models of kittiwake reproductive success. Performance of multiple variable generalized linear mixed effects models explaining the probability of chick production at Black-legged Kittiwake colonies in Prince William Sound, AK, during 1985-2012, with year and colony as random effects. The global model was of the form Pr(chick production) ~ climate + population density + precipitation + fish + depth + wind + colony size. Models in the "global minus one" set tested the ability of each variable to improve the model by comparing model performance of the global model versus the model with each individual variable removed. Boldface type indicates models that performed worse than the global model due to the omission of influential variables. Models in the "key variables" set explored the relative contribution of variables whose omission worsened the global model's performance by <2.0 ΔAIC units. Asterisk denotes the best-supported model based on a combination of AIC score, ANOVA comparison among competitive models, and validation using held out data.

Set	Model	AIC	ΔAIC (from global)	w_i	deviance	k	ANOVA
GLOBAL MINUS ONE	*global - climate*	526.10	-1.51	0.09	508.10	9	
	global - competition	526.37	-1.24	0.07	508.37	9	
	global - rain	526.99	-0.62	0.05	508.99	9	
	global	527.61	0.00	0.04	507.61	10	
	global - fish	527.90	0.30	0.03	509.90	9	p = 0.13 (with global model)
	global - depth	528.08	0.47	0.03	510.08	9	p = 0.12 (with global model)
	global - wind	532.50	4.90	0.00	514.50	9	
	global - col. size	544.76	17.15	0.00	526.76	9	
KEY VARIABLES	*col. size + wind + depth + fish*	523.84	-3.77	0.27	509.84	7	
	** col. size + wind + depth*	524.19	-3.42	0.22	512.19	6	p = 0.13 (with top model)
	col. size + wind + fish	525.73	-1.87	0.10	513.73	6	p = 0.05 (with top model)
	col. size + wind	526.12	-1.49	0.08	516.12	5	

Table A5. Single variable models of kittiwake reproductive success. Performance of single variable linear mixed effects models explaining productivity at Black-legged Kittiwake colonies in Prince William Sound, AK, during 1985-2012, with colony and year as random effects. Boldface type indicates top-scoring variables from each group that were used in subsequent multi-variable modeling. Akaike weights are denoted by wi, and k represents the number of model parameters.

Group	Variable	AIC	ΔAIC (overall)	ΔAIC (within group)	w_i (within group)	deviance	k
Colony size	**Number of nests at each colony in each year**	6.45	142.31	0.00	1.00	-3.55	5
Inter-colony competition	**Density of kittiwake pairs within foraging range of colony**	-1.05	134.82	0.00	1.00	-11.05	5
Foraging area	**Total area within foraging range of colony**	2.80	138.67	0.00	0.64	-7.20	5
	Ratio of shoreline area (<401m from land) to total area within foraging range of colony	4.91	140.78	2.11	0.22	-5.09	5
	Total shoreline area (<401m from land) within foraging range of colony	6.00	141.86	3.19	0.13	-4.00	5
Depth	**Median depth within 45 km foraging range of colony**	2.13	137.99	0.00	0.54	-7.87	5
	Number of raster points representing depth <31m within foraging range of colony	2.85	138.71	0.72	0.37	-7.15	5
	Mean depth within foraging range of colony	5.70	141.56	3.57	0.09	-4.30	5
Fish	**Number of herring spawn raster points within foraging range of colony in current year**	3.89	139.76	0.00	0.25	-6.11	5
	Number of herring spawn raster points within foraging range of colony in previous year	3.91	139.77	0.02	0.25	-6.09	5
	Modeled number of age 1 herring (one value for whole region)	6.09	141.95	2.20	0.08	-3.91	5
	Number of age 1 salmon released in colony subdistrict	4.53	140.39	0.64	0.18	-5.47	5
	Number of age 1 and age 2 salmon released in colony subdistrict	4.66	140.53	0.77	0.17	-5.34	5
	Salmon density within foraging range of colony	6.60	142.47	2.71	0.06	-3.40	5
Predation	**Intra-colony plot-level coefficient of variation in fledging brood size**	-135.86	0.00	0.00	1.00	-145.86	5
Precipitation	**Total July precipitation (mm; colony-specific)**	0.19	136.06	0.00	0.49	-9.81	5
	Number of July days with precipitation > 14mm (colony-specific)	1.56	137.42	1.36	0.25	-8.44	5
	Number of June days with precipitation > 14mm (colony-specific)	2.88	138.74	2.68	0.13	-7.12	5
	Number of July days with precipitation > 0mm (colony-specific)	4.08	139.94	3.89	0.07	-5.92	5
	Total June precipitation (mm; colony-specific)	5.15	141.02	4.96	0.04	-4.85	5
	Number of June days with precipitation > 0mm (colony-specific)	6.32	142.18	6.13	0.02	-3.68	5
Wind	**Average July wind magnitude (one value for whole region)**	3.96	139.83	0.00	0.27	-6.04	5
	Average July N/S wind magnitude (one value for whole region)	4.37	140.23	0.40	0.22	-5.63	5
	Average July E/W wind magnitude (one value for whole region)	4.66	140.53	0.70	0.19	-5.34	5
	Average directional July N/S wind (one value for whole region)	4.75	140.61	0.78	0.18	-5.25	5
	Average directional July E/W wind (one value for whole region)	5.35	141.21	1.38	0.14	-4.65	5
SST	**Modeled mean May sea surface temperature (one value for whole region)**	5.19	141.05	0.00	1.00	-4.81	5
Climate	**Average December-February ENSO Nino 3.4 index value (one value for whole region)**	3.61	139.48	0.00	0.45	-6.39	5
	May Pacific Decadal Oscillation index value (one value for whole region)	5.40	141.27	1.79	0.18	-4.60	5
	June Pacific Decadal Oscillation index value (one value for whole region)	5.82	141.68	2.21	0.15	-4.18	5
	July Pacific Decadal Oscillation index value (one value for whole region)	6.29	142.15	2.67	0.12	-3.71	5
	April Pacific Decadal Oscillation index value (one value for whole region)	6.59	142.46	2.98	0.10	-3.41	5
Null	Intercept-only model	4.60	140.47	0.00	1.00	-3.40	4

Table A6. Multiple variable models of kittiwake reproductive output. Performance of multiple variable generalized linear mixed effects models explaining the reproductive output, given success, at Black-legged Kittiwake colonies in Prince William Sound, AK, during 1985-2012, including the brood size variability metric, with colony as a random effect. The global model was of the form $productivity^{0.4} \sim predation + population\ density + fish + colony\ size + climate + rain + wind + depth + SST + area$. Models in the "global minus one" set tested the ability of each variable to improve the model by comparing model performance of the global model versus the model with each individual variable removed. Boldface type indicates models that performed worse than the global model due to the omission of influential variables. Models in the "key variables" set explored the relative contribution of variables whose omission worsened the global model's performance by <2.0 ΔAIC units. Asterisk denotes the best-supported model based on a combination of AIC score, ANOVA comparison among competitive models, and validation using held out data.

Set	Model	AIC	ΔAIC (from global)	w_i	deviance	k	ANOVA
GLOBAL MINUS ONE	*global - wind*	-147.861	-1.88	0.05	-173.86	13	
	global - SST	-147.791	-1.81	0.05	-173.79	13	
	global - area	-147.757	-1.77	0.05	-173.76	13	
	global - depth	-146.815	-0.83	0.03	-172.82	13	
	global	-145.986	0.00	0.02	-173.99	14	
	global - winter ENSO	-145.209	0.78	0.01	-171.21	13	p = 0.096 (with global model)
	global - rain	-144.382	1.60	0.01	-170.38	13	p = 0.058 (with global model)
	global - colony size	-143.935	2.05	0.01	-169.93	13	
	global - fish	-141.665	4.32	0.00	-167.67	13	
	global - competition	-137.907	8.08	0.00	-163.91	13	
	global - predation	-7.05539	138.93	0.00	-33.06	13	
KEY VARIABLES	*predation + competition + fish + col. size + rain + winter ENSO*	-152.191	-6.20	0.43	-172.19	10	
	** predation + competition + fish + col. size + rain*	-150.855	-4.87	0.22	-168.86	9	p = 0.068 (with top model)
	predation + competition + fish + col. size + winter ENSO	-148.836	-2.85	0.08	-166.84	9	
	predation + competition + fish + col. size	-148.054	-2.07	0.05	-164.05	8	

Table A7. Single variable models of tern reproductive output. Performance of single variable linear mixed effects models explaining reproductive output, given success, at managed Common Tern colonies in the Gulf of Maine during 2001-2016, with colony and year as random effects. Boldface type indicates top-scoring variables from each group that were used in subsequent multi-variable modeling. Akaike weights are denoted by wi, and k represents the number of model parameters.

Group	Variable	AIC	ΔAIC (overall)	ΔAIC (within group)	w_i (within group)	deviance	k
Colony size	**Number of nests at each colony in each year**	226.48	13.85	0.00	1.00	216.48	5
Population density	**Density of breeding tern pairs within foraging range of colony (includes overlapping colony ranges)**	212.63	0.00	0.00	1.00	202.63	5
Foraging area	**Total area within foraging range of colony**	221.50	8.86	0.00	0.53	211.50	5
	Ratio of shoreline area (<401m from land) to total area within foraging range of colony	223.01	10.38	1.51	0.25	213.01	5
	Total shoreline area (<401m from land) within foraging range of colony	223.25	10.62	1.75	0.22	213.25	5
Depth	**Mean depth within foraging range of colony**	216.18	3.55	0.00	0.75	206.18	5
	Median depth within foraging range of colony	219.35	6.72	3.17	0.15	209.35	5
	Number of raster points representing depth <18.3 m within foraging range of colony	220.31	7.68	4.14	0.09	210.31	5
Fish	**Frequency of combined herring and silver hake with length > 140 mm within foraging range of colony**	222.51	9.88	0.00	0.41	212.51	5
	Frequency of silver hake with length > 140 mm per tow within foraging range of colony	223.12	10.49	0.61	0.30	213.12	5
	Frequency of combined herring and silver hake with length < 140 mm within foraging range of colony	225.48	12.85	2.97	0.09	215.48	5
	Frequency of herring with length < 140 mm per tow within foraging range of colony	225.65	13.01	3.14	0.08	215.65	5
	Frequency of silver hake with length < 140 mm per tow within foraging range of colony	226.22	13.59	3.71	0.06	216.22	5
	Frequency of herring with length >140 mm per tow within foraging range of colony	226.49	13.85	3.98	0.06	216.49	5
Precipitation	**Number of July days with precipitation > 0mm (colony-specific)**	224.40	11.77	0.00	0.30	214.40	5
	Total June precipitation (colony-specific)	225.22	12.59	0.82	0.20	215.22	5
	Total July precipitation (colony-specific)	225.85	13.22	1.46	0.15	215.85	5
	Number of July days with precipitation > 14mm (colony-specific)	226.04	13.41	1.64	0.13	216.04	5
	Number of June days with precipitation > 14mm (colony-specific)	226.38	13.75	1.99	0.11	216.38	5
	Number of June days with precipitation > 0mm (colony-specific)	226.46	13.83	2.06	0.11	216.46	5

Table A7 continued

Group	Variable	AIC	ΔAIC (overall)	ΔAIC (within group)	w_i (within group)	deviance	k
Wind	**Average June NE wind magnitude (one value for whole region)**	223.55	10.91	0.00	0.23	213.55	5
	Average directional July N/S wind (one value for whole region)	224.12	11.49	0.57	0.18	214.12	5
	Average July N/S wind magnitude (one value for whole region)	224.12	11.49	0.57	0.18	214.12	5
	Average July NE wind magnitude (one value for whole region)	224.55	11.92	1.00	0.14	214.55	5
	Average July wind magnitude (one value for whole region)	225.30	12.67	1.75	0.10	215.30	5
	Average directional July E/W wind (one value for whole region)	226.25	13.62	2.71	0.06	216.25	5
	Average July E/W wind magnitude (one value for whole region)	226.25	13.62	2.71	0.06	216.25	5
	Average May NE wind magnitude (one value for whole region)	226.31	13.68	2.77	0.06	216.31	5
SST	**Average May SST (one value for whole region)**	220.31	7.68	0.00	0.51	210.31	5
	Average July SST (one value for whole region)	221.44	8.81	1.13	0.29	211.44	5
	Average June SST (one value for whole region)	222.24	9.61	1.93	0.20	212.24	5
Climate	**July NAO index value (one value for whole region)**	221.85	9.22	0.00	0.41	211.85	5
	June NAO index value (one value for whole region)	224.02	11.39	2.17	0.14	214.02	5
	Average December-February AMO index value (one value for whole region)	225.06	12.43	3.22	0.08	215.06	5
	April AMO index value (one value for whole region)	225.61	12.98	3.76	0.06	215.61	5
	June AMO index value (one value for whole region)	226.08	13.45	4.23	0.05	216.08	5
	Average December-February NAO index value (one value for whole region)	226.16	13.53	4.32	0.05	216.16	5
	Average December-February ENSO Nino 3.4 index value (one value for whole region)	226.33	13.70	4.48	0.04	216.33	5
	July AMO index value (one value for whole region)	226.35	13.72	4.50	0.04	216.35	5
	May NAO index value (one value for whole region)	226.46	13.83	4.62	0.04	216.46	5
	April NAO index value (one value for whole region)	226.47	13.84	4.63	0.04	216.47	5
	May AMO index value (one value for whole region)	226.48	13.85	4.63	0.04	216.48	5
Null	Intercept-only model	224.49	11.85	0.00	1.00	216.49	4

Table A8. Multiple variable models of tern reproductive output. Performance of multiple variable linear mixed effects models explaining reproductive output, given success, at Common Tern colonies in the Gulf of Maine during 2001-2016, with colony and year as random effects. The global model was of the form productivity ~ population density + depth + colony size + wind + area + SST + fish + climate + rain. Models in the "global minus one" set tested the ability of each variable to improve the model by comparing model performance of the global model versus the model with each individual variable removed. Boldface type indicates models that performed worse than the global model due to the omission of influential variables. Models in the "key variables" set explored the relative contribution of variables whose omission worsened the global model's performance by <2.0 ΔAIC units. Asterisk denotes the best-supported model based on a combination of AIC score, ANOVA comparison among competitive models, and validation using held out data.

Set	Model	AIC	ΔAIC (from global)	w_i	deviance	k	ANOVA
GLOBAL MINUS ONE	*global - rain*	197.21	-1.98	0.093	173.21	12	
	global - fish	197.69	-1.49	0.073	173.69	12	
	global - climate	197.90	-1.28	0.066	173.90	12	
	global	199.19	0.00	0.035	173.19	13	
	global - area	199.74	0.55	0.026	175.74	12	p = 0.110 (with global model)
	global - SST	199.75	0.57	0.026	175.75	12	p = 0.109 (with global model)
	global - wind	200.22	1.04	0.021	176.22	12	p = 0.081 (with global model)
	global - col. size	203.96	4.77	0.003	179.96	12	
	global - depth	204.35	5.16	0.003	180.35	12	
	global - pop. density	215.92	16.74	<0.001	191.92	12	
KEY VARIABLES	*pop. density + depth + col. size + wind + SST + area*	194.72	-4.47	0.323	174.72	10	
	** pop. density + depth + col. size + wind + SST*	195.47	-3.71	0.221	177.47	9	p = 0.097 (with top model)
	pop. density + depth + col. size + wind	197.70	-1.49	0.073	181.70	8	p = 0.031 (with top model)
	pop. density + depth + col. size	199.02	-0.17	0.038	185.02	7	

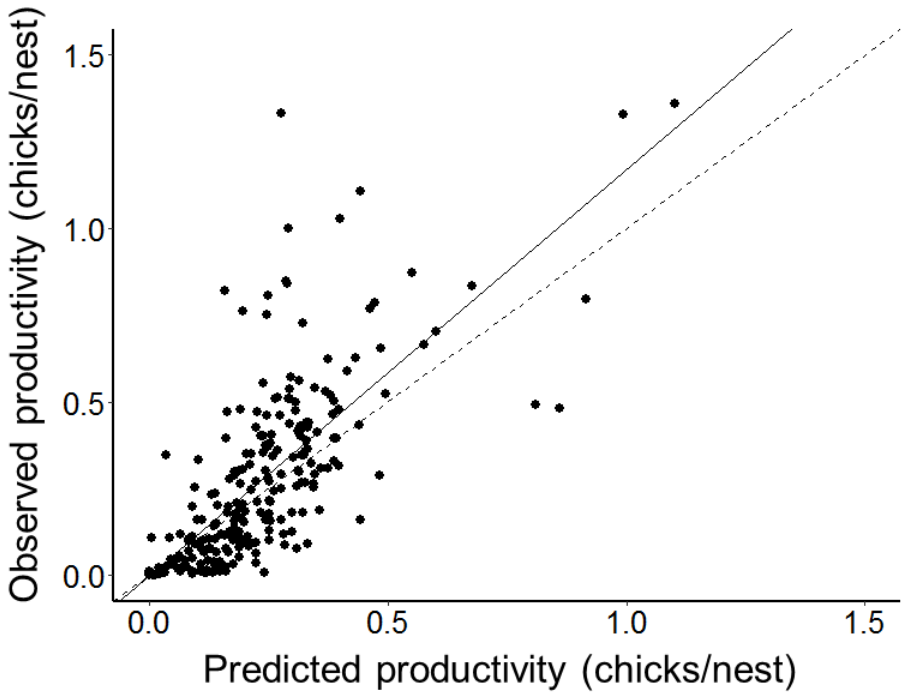

Figure A1. Kittiwake training dataset regression. Observed vs. fitted value regression using training dataset and coefficients from the top model predicting reproductive output, given reproductive success, for Black –legged Kittiwake colonies in Prince William Sound, AK from 1985-2012. Dotted line represents perfect estimation (y = x).

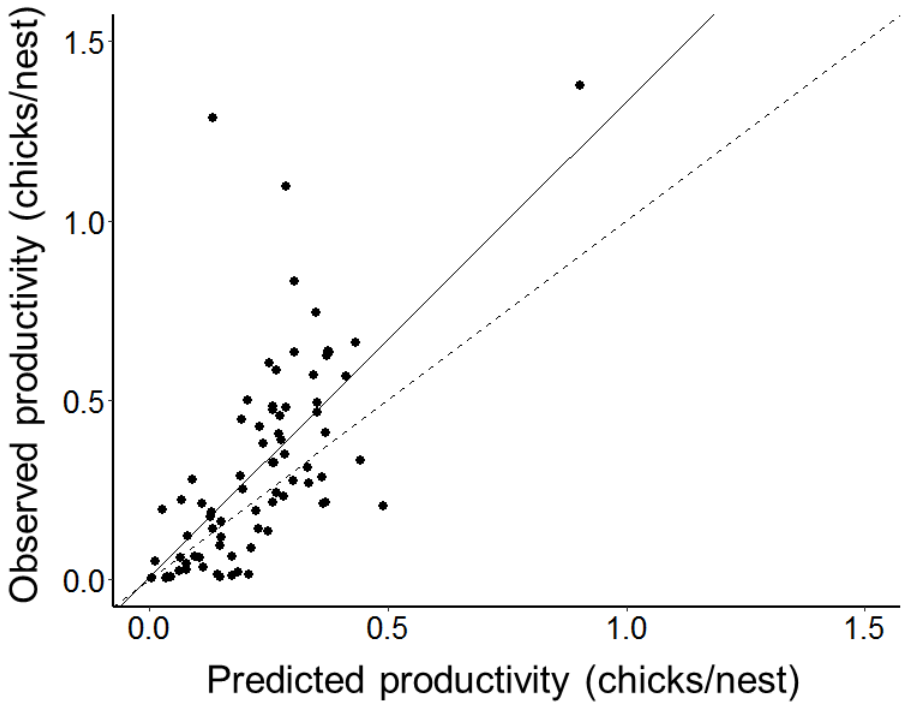

Figure A2. Kittiwake validation dataset regression. Observed vs. fitted value regression using validation dataset and coefficients from the top model predicting reproductive output, given reproductive success, for Black –legged Kittiwake colonies in Prince William Sound, AK from 1985-2012. Dotted line represents perfect estimation (y = x).

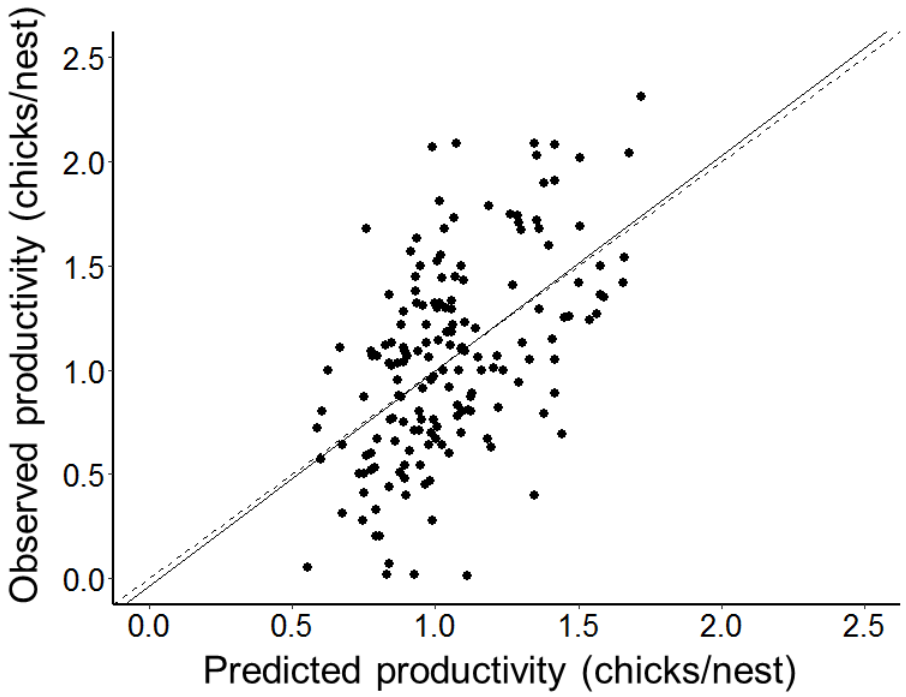

Figure A3. Tern training dataset regression. Observed vs. fitted value regression using training dataset and coefficients from the top model predicting reproductive output, given reproductive success, for Common Tern colonies in the Gulf of Maine from 2001-2016. Dotted line represents perfect estimation (y = x).

Appendix B: Supplementary Information for Chapter 3

Table B1. Single variable models of kittiwake laying success. Performance of single variable generalized linear mixed effects models explaining the probability of laying success at a Black-legged Kittiwake colony in Prince William Sound, AK from 1996-2008, with individual ID and nested year and colony section as random effects. "Winter" refers to monthly values from November through February prior to the breeding season; "spring" refers to monthly values from March to April prior to the breeding season. Top-ranked variables within each group that outperformed the null model and were not correlated ($r \geq 0.65$) with a higher ranked representative variable were used in subsequent modeling (boldface type); asterisks indicate variables that met two of these criteria but were unusable due to correlation with higher ranked representative variables. Akaike weights are denoted by wi, and k represents the number of model parameters.

Group	Model	AIC	ΔAIC	w_i	deviance	k
Age	***age***	1420.42	0.00	>0.99	1412	4
Colony size	***colony size***	1476.95	56.53	<0.01	1469	4
Phenology	***median first egg lay date***	1467.99	47.57	<0.01	1460	4
	median first chick hatch date	1473.63	53.21	<0.01	1466	4
Condition	***average incubation body condition***	1488.87	68.45	<0.01	1481	4
Previous productivity	***productivity in previous year***	1492.85	72.43	<0.01	1485	4
Winter wind	*winter N/S wind magnitude**	1480.05	59.63	<0.01	1472	4
	winter directional N/S wind	1484.53	64.11	<0.01	1477	4
	winter wind magnitude	1485.22	64.80	<0.01	1477	4
	winter E/W wind magnitude	1487.45	67.03	<0.01	1479	4
	winter directional E/W wind	1492.16	71.74	<0.01	1484	4
Spring wind	***spring wind magnitude***	1488.56	68.14	<0.01	1481	4
	spring E/W wind magnitude	1490.82	70.40	<0.01	1483	4
	spring directional N/S wind	1491.80	71.38	<0.01	1484	4
	spring directional E/W wind	1492.40	71.98	<0.01	1484	4
	spring N/S wind magnitude	1492.49	72.07	<0.01	1484	4
Winter SST	*PWS winter maximum monthly SST**	1491.20	70.78	<0.01	1483	4
	*GOA winter maximum monthly SST**	1493.70	73.28	<0.01	1486	4
	*GOA winter monthly mean SST**	1494.22	73.80	<0.01	1486	4
	PWS winter monthly mean SST	1494.72	74.30	<0.01	1487	4
April SST	*PWS April SST*	1494.83	74.41	<0.01	1487	4
	GOA April SST	1495.04	74.62	<0.01	1487	4
Climate	***mean winter Niño 3.4 index value***	1489.97	69.55	<0.01	1482	4
	mean winter PDO index value	1494.75	74.33	<0.01	1487	4
Null	*intercept only*	1493.12	72.70	<0.01	1487	3

Table B2. Multiple variable models of kittiwake laying success. Performance of multiple variable generalized linear mixed effects models explaining the probability of laying success at a Black-legged Kittiwake colony in Prince William Sound, AK from 1996-2008, with individual ID and nested year and colony section as random effects. "Winter" refers to monthly values from November through February prior to the breeding season; "spring" refers to monthly values from March to April prior to the breeding season. The global model was of the form Pr(eggs) ~ age + phenology + climate + colony size + condition + spring wind. Models in the "global minus one" set tested the ability of each variable to improve the model by comparing model performance of the global model versus the model with each individual variable removed. Boldface type indicates models that performed worse than the global model due to the omission of influential variables. Models in the "key variables" set explored the relative contribution of variables whose omission worsened the global model's performance by <2.0 ΔAIC units. Asterisk denotes the best-supported model based on a combination of AIC score, ANOVA comparison among competitive models, and validation using non-individually identifiable data. Akaike weights are denoted by wi, and k represents the number of model parameters.

Set	**Model**	**AIC**	**ΔAIC (from global)**	**w_i**	**deviance**	**k**	**ANOVA**
Global minus one	*global - spring wind*	1381.72	-1.77	0.27	1366	8	
	global - condition	1383.46	-0.03	0.11	1367	8	
	global	1383.49	0.00	0.11	1365	9	
	global - colony size	1385.02	1.53	0.05	1369	8	p = 0.06 (with global model)
	global - climate	1390.91	7.41	0.00	1375	8	
	global - phenology	1391.50	8.00	0.00	1375	8	
	global - age	1467.18	83.69	0.00	1451	8	
Key variables	*age + phenology + climate + colony size*	1381.50	-1.99	0.30	1368	7	
	** age + phenology + climate*	1383.00	-0.49	0.14	1371	6	p = 0.06 (with best model)

Table B3. Top laying success model coefficients. Fixed effect coefficients and random effect variance and standard error from the best-performing model of Black-legged Kittiwake laying success at the Shoup Bay colony in Prince William Sound, AK from 1996-2008.

FIXED EFFECTS

Coefficient	**Estimate**	**SE**	**z**	**p**
intercept	-0.35	0.22	-1.57	0.12
age	0.25	0.03	8.02	<0.001
phenology	-0.83	0.12	-6.67	<0.001
climate	0.42	0.12	3.43	<0.001

RANDOM EFFECTS

Intercept	**Variance**	**SE**
Individual bird ID	0.22	0.47
Colony section nested within year	0.30	0.55

Table B4. Single variable models of kittiwake hatching success. Performance of single variable generalized linear mixed effects models explaining the probability of hatching success at a Black-legged Kittiwake colony in Prince William Sound, AK from 1996-2008, with individual ID and nested year and colony section as random effects. "Winter" refers to monthly values from November through February prior to the breeding season; "spring" refers to monthly values from March to April prior to the breeding season. Top-ranked variables within each group that outperformed the null model and were not correlated ($r \geq 0.65$) with a higher ranked representative variable were used in subsequent modeling (boldface type); asterisks indicate variables that met two of these criteria but were unusable due to correlation with higher ranked representative variables. Akaike weights are denoted by wi, and k represents the number of model parameters.

Group	Model	AIC	ΔAIC	w_i	deviance	k
Age	***age***	1490.73	2.61	0.07	1483	4
Colony size	***colony size***	1488.73	0.61	0.20	1481	4
Phenology	***median first egg lay date***	1495.48	7.36	0.01	1487	4
	median first chick hatch date	1497.96	9.85	<0.01	1490	4
Condition	***average incubation body condition***	1490.14	2.02	0.10	1482	4
Previous productivity	***productivity in previous year***	1496.38	8.26	<0.01	1488	4
Winter wind	***winter E/W wind magnitude***	1489.33	1.21	0.15	1481	4
	winter directional N/S wind	1491.94	3.82	0.04	1484	4
	winter wind magnitude	1494.13	6.01	0.01	1486	4
	winter N/S wind magnitude	1496.38	8.26	<0.01	1488	4
	winter directional E/W wind	1498.51	10.39	<0.01	1491	4
Spring wind	***spring directional E/W wind***	1494.00	5.88	0.01	1486	4
	spring directional N/S wind	1495.30	7.18	0.01	1487	4
	spring N/S wind magnitude	1495.67	7.55	0.01	1488	4
	spring E/W wind magnitude	1497.70	9.59	<0.01	1490	4
	spring wind magnitude	1498.31	10.19	<0.01	1490	4
Winter SST	*PWS winter maximum monthly SST**	1494.66	6.54	0.01	1487	4
	*GOA winter maximum monthly SST**	1495.48	7.36	0.01	1487	4
	GOA winter monthly mean SST	1498.34	10.22	<0.01	1490	4
	PWS winter monthly mean SST	1498.49	10.37	<0.01	1490	4
April SST	*PWS April SST*	1498.37	10.25	<0.01	1490	4
	GOA April SST	1498.53	10.41	<0.01	1491	4
Precipitation	*maximum daily July precipitation*	1498.01	9.89	<0.01	1490	4
	number of days with precipitation >2.54mm	1498.17	10.05	<0.01	1490	4
	total July precipitation	1498.32	10.20	<0.01	1490	4
Temperature	*July mean maximum daily air temperature*	1498.39	10.28	<0.01	1490	4
	July mean daily air temperature	1498.45	10.33	<0.01	1490	4
Climate	*mean winter PDO index value*	1498.41	10.29	<0.01	1490	4
	mean winter Niño 3.4 index value	1498.50	10.38	<0.01	1491	4
Salmon timing	***date salmon landings exceed 30,000 fish***	1488.12	0.00	0.27	1480	4
	date salmon landings exceed one million fish	1491.15	3.03	0.06	1483	4
	total salmon landings	1497.53	9.41	<0.01	1490	4
Null	*intercept only*	1496.55	8.43	<0.01	1491	3

Table B5. Multiple variable models of kittiwake hatching success. Performance of multiple variable generalized linear mixed effects models explaining the probability of hatching success at a Black-legged Kittiwake colony in Prince William Sound, AK from 1996-2008, with individual ID and nested year and colony section as random effects. "Winter" refers to monthly values from November through February prior to the breeding season; "spring" refers to monthly values from March to April prior to the breeding season. The global model was of the form Pr(chicks) ~ age + salmon timing + condition + phenology + winter wind + previous productivity + spring wind + colony size. Models in the "global minus one" set tested the ability of each variable to improve the model by comparing model performance of the global model versus the model with each individual variable removed. Boldface type indicates models that performed worse than the global model due to the omission of influential variables. Asterisk denotes the final model formulation containing only those fixed effects whose omission significantly increased the AIC score of the global model. Akaike weights are denoted by wi, and k represents the number of model parameters.

Set	**Model**	**AIC**	**ΔAIC (from global)**	**w_i**	**deviance**	**k**
Global minus one	*global - colony size*	1481.50	-1.92	0.15	1462	10
	global - spring wind	1481.54	-1.88	0.15	1462	10
	global - previous productivity	1481.85	-1.57	0.13	1462	10
	global - winter wind	1481.90	-1.52	0.13	1462	10
	global - phenology	1482.13	-1.30	0.11	1462	10
	global - condition	1482.19	-1.23	0.11	1462	10
	global	1483.42	0.00	0.06	1461	11
	global - salmon timing	1486.34	2.92	0.01	1466	10
	global - age	1487.71	4.28	0.01	1468	10
Final model	** age + salmon timing*	1481.66	-1.76	0.14	1472	5

Table B6. Top hatching success model coefficients. Fixed effect coefficients and random effect variance and standard error from top model of Black-legged Kittiwake hatching success at the Shoup Bay colony in Prince William Sound, AK from 1996-2008.

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FIXED EFFECTS

Coefficient	**Estimate**	**SE**	**z**	**p**
intercept	-1.29	0.29	-4.48	<0.001
age	0.07	0.02	2.91	0.004
salmon timing	-0.84	0.25	-3.36	<0.001

RANDOM EFFECTS

Intercept	**Variance**	**SE**
Individual bird ID	0.13	0.37
Colony section nested within year	1.84	1.36

Appendix C: Supplementary Information for Chapter 4

Table C1. Survival models. Performance of multi-state models estimating the probability of survival (φ) for black-legged kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010. Model structure for transition probability was held constant as state X time, and resight model structure was set to the best competing structure from Table 3. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis.

Model	Hypothesis	$\Delta QAICc$	w_i	K
$\varphi_{(state + trend)}$	Survival varies between states with a trend over time.	0.00	0.33	34
$\varphi_{(PDO + state + trend)}$	Survival varies between states and among PDO index values with a trend over time. PDO is a time-varying value common to all individuals within each year.	0.19	0.30	35
$\varphi_{(manip + state + trend)}$	Survival varies between states and between treatment groups with a trend over time.	1.93	0.13	35
$\varphi_{(prod + state + trend)}$	Survival varies between states and among colony productivity values with a trend over time. Colony productivity is a time-varying value common to all individuals within each year.	1.98	0.12	35
$\varphi_{(qual + state + trend)}$	Survival varies between states and among quality categories with a trend over time.	2.82	0.08	36
$\varphi_{(state X period)}$	Survival varies between states and among early, mid-, and late post-experimental periods, with a different period pattern between states.	6.56	0.01	36
$\varphi_{(state + prod)}$	Survival varies between breeding states and among colony productivity values. Colony productivity is a time-varying value common to all individuals within a year.	8.64	0.00	34
$\varphi_{(state X PDO)}$	Survival varies between breeding states and among winter PDO index values, with a different PDO pattern between states. PDO is a time-varying value common to all	9.01	0.00	35
$\varphi_{(state + PDO)}$	Survival varies only in relation to breeding state + PDO.	9.44	0.00	34
$\varphi_{(state X prod)}$	Survival varies between breeding states and among colony productivity values, with a different productivity pattern between states. Colony productivity is a time-varying value common to all individuals within a year.	9.60	0.00	35
$\varphi_{(state X period)}$	Survival varies between states and among early, mid-, and late post-experimental periods, with a different period pattern between states.	9.62	0.00	39
$\varphi_{(state)}$	Survival varies only in relation to breeding state.	11.77	0.00	33
$\varphi_{(state + time)}$	Survival varies between breeding states and among years.	18.53	0.00	47
$\varphi_{(time)}$	Survival varies only in relation to time.	25.60	0.00	46
$\varphi_{(prod)}$	Survival varies among colony productivity values. Colony productivity is a time-varying value common to all individuals within a year.	29.04	0.00	33
$\varphi_{(PDO)}$	Survival varies only in relation to winter PDO index values. PDO is a time-varying value common to all individuals within each year.	33.27	0.00	33
$\varphi_{(constant)}$	Survival does not vary.	35.59	0.00	32
$\varphi_{(state X time)}$	Survival varies between breeding states and among years, with a different yearly pattern between states.	38.97	0.00	61

Table C2. Top survival model coefficients. Coefficient values for survival parameters in the top-ranked survival model structure for kittiwakes involved in a long-term cost of reproduction experiment at the Shoup Bay colony in Prince William Sound, Alaska. The top-ranked model did not include the manipulation term, indicating that forced nest failures during 1991-1994 had little effect on long-term survival.

Beta	Estimate	SE	85% CI		Significant
intercept	2.62	0.26	2.25	2.99	*
state	0.69	0.25	0.33	1.05	*
time trend	-0.09	0.02	-0.13	-0.06	*

Table C3. Breeding state transition models. Performance of competing structures for multi-state models estimating the probability of transition (Ψ) between breeding and non-breeding states for Black-legged Kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010. Model structure for survival was held constant as state X time, and resight model structure was set to the best competing structure from Table 3. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis.

Model	**Hypothesis**	**$\Delta QAIC_c$**
$\Psi_{(manip + state X time)}$	Nonbreeding varies between treatment groups, between breeding states, and among years, with a different yearly pattern between states.	0.00
$\Psi_{(cmanip + state X time)}$	Nonbreeding varies between binary treatment categories, between breeding states, and among years, with a different yearly pattern between states.	2.06
$\Psi_{(state X time)}$	Nonbreeding varies between breeding states, among years, and with a different yearly pattern between states.	2.57
$\Psi_{(quality + state X time)}$	Nonbreeding varies among birds of different quality, between breeding states, and among years, with a different yearly pattern between states.	5.43
$\Psi_{(tmanip + state X time)}$	Nonbreeding varies between between treatment groups, between breeding states and among years, with a different yearly pattern between states and differing magnitudes of the treatment effect over time.	21.41
$\Psi_{(state + time)}$	Nonbreeding varies between breeding states and among years.	21.79
$\Psi_{(state + period)}$	Nonbreeding varies between breeding states and among early, mid-, and late post-experimental time periods.	42.47
$\Psi_{(state X prod)}$	Nonbreeding varies between breeding states, among colony productivity rates, with a different productivity pattern between states. Colony productivity is a time-varying value common to all individuals within a year.	101.87
$\Psi_{(state + prod)}$	Nonbreeding varies between breeding states and among colony productivity rates. Colony productivity is a time-varying value common to all individuals within a year.	108.06
$\Psi_{(state + PDO)}$	Nonbreeding varies between breeding states and among PDO index values. PDO is a time-varying value common to all individuals within each year.	140.02
$\Psi_{(state X PDO)}$	Nonbreeding varies by breeding state and among PDO index values, with a different PDO pattern between states. PDO is a time-varying value common to all individuals within each year.	140.02

Table C4. Top transition model coefficients. Coefficient values for transition parameters in the top-ranked transition model structure for kittiwakes involved in a long-term cost of reproduction experiment at the Shoup Bay colony in Prince William Sound, Alaska. The top-ranked model included the manipulation term, indicating that forced nest failures during 1991-1994 increased the probability of breeding over the long term.

Beta	**Estimate**	**SE**	**85% CI**		**Significant**	**Comments**
intercept	2.10	0.57	1.29	2.92	*	
state	-1.23	1.19	-2.94	0.48		
manip	-0.13	0.06	-0.21	-0.04	*	
1995	-0.10	0.00	-0.10	-0.10	*	*fixed*
1996	-0.99	0.68	-1.97	-0.02	*	
1997	-1.26	0.67	-2.22	-0.30	*	
1998	-1.29	0.64	-2.22	-0.37	*	
1999	-1.34	0.63	-2.25	-0.43	*	
2000	-0.44	0.66	-1.39	0.52		
2001	-1.33	0.61	-2.21	-0.45	*	
2002	-0.92	0.63	-1.83	-0.02	*	
2003	-1.21	0.62	-2.11	-0.32	*	
2004	-0.82	0.64	-1.74	0.11		
2005	0.39	0.73	-0.66	1.44		
2006	-1.06	0.63	-1.96	-0.16	*	
2007	-0.47	0.69	-1.46	0.51		
2008	-0.96	0.68	-1.93	0.01		
2009	0.30	0.88	-0.97	1.56		*confounded*
state X 1995	-0.10	0.00	-0.10	-0.10	*	*fixed*
state X 1996	-2.33	1.28	-4.17	-0.48	*	
state X 1997	-1.05	1.26	-2.86	0.76		
state X 1998	-0.71	1.24	-2.50	1.08		
state X 1999	-0.52	1.24	-2.30	1.27		
state X 2000	-0.65	1.25	-2.46	1.15		
state X 2001	0.13	1.24	-1.65	1.91		
state X 2002	0.00	1.24	-1.79	1.80		
state X 2003	0.46	1.25	-1.33	2.26		
state X 2004	0.31	1.26	-1.51	2.13		
state X 2005	0.28	1.35	-1.66	2.21		
state X 2006	1.24	1.39	-0.77	3.24		
state X 2007	0.31	1.33	-1.60	2.23		
state X 2008	-0.11	1.36	-2.06	1.85		
state X 2009	0.95	1.56	-1.29	3.19		*confounded*

Table C5. Tag loss sensitivity analysis: resight probability models. Performance of multi-state models estimating the encounter probability (p) for black-legged kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010 with all individuals with degraded marks and reconstructed identities removed. Model structures for survival and transition probability were held constant as state X time. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis.

Model	**$\Delta QAIC_c$**	**w_i**	**K**
$p_{(state)}$	0.00	1.00	64
$p_{(state + time)}$	15.36	0.00	79
$p_{(state X time)}$	42.94	0.00	94
$p_{(time)}$	143.92	0.00	78
$p_{(constant)}$	146.22	0.00	63

Table C6. Tag loss sensitivity analysis: survival models. Performance of multi-state models estimating the probability of survival (φ) for black-legged kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010 with all individuals with degraded marks and reconstructed identities removed. Model structure for transition probability was held constant as state X time, and resight model structure was set to the best competing structure from Table S5. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. Significance of covariate effects noted in comments for competitive models.

Model	**$\Delta QAIC_c$**	**w_i**	**K**	**Comments**
$\varphi_{(state + time)}$	0.00	0.29	47	
$\varphi_{(state + time + cmanip)}$	1.81	0.12	48	Manipulation effect insignificant
$\varphi_{(state + time + qual)}$	1.91	0.11	48	Quality effect insignificant
$\varphi_{(state + time + manip)}$	2.06	0.10	48	Manipulation effect insignificant
$\varphi_{(time)}$	3.29	0.06	46	
$\varphi_{(PDO + state + trend)}$	4.71	0.03	35	
$\varphi_{(state + trend)}$	4.89	0.03	34	
$\varphi_{(trend)}$	6.44	0.01	33	
$\varphi_{(prod + state + trend)}$	6.53	0.01	35	
$\varphi_{(cmanip + state + trend)}$	6.66	0.01	35	
$\varphi_{(qual + state + trend)}$	6.73	0.01	35	
$\varphi_{(manip + state + trend)}$	6.92	0.01	35	
$\varphi_{(state X prod)}$	21.25	0.00	35	
$\varphi_{(state X time)}$	21.79	0.00	61	
$\varphi_{(state + PDO)}$	24.12	0.00	34	
$\varphi_{(state X PDO)}$	24.38	0.00	35	
$\varphi_{(state)}$	25.94	0.00	33	
$\varphi_{(state X manip)}$	29.53	0.00	35	
$\varphi_{(state X cmanip)}$	29.75	0.00	35	
$\varphi_{(prod)}$	34.84	0.00	33	
$\varphi_{(PDO)}$	40.95	0.00	33	
$\varphi_{(constant)}$	43.36	0.00	32	

Table C7. Tag loss sensitivity analysis: transition models. Performance of competing structures for multi-state models estimating the probability of transition (Ψ) between breeding and non-breeding states for Black-legged Kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010 with all individuals with degraded marks and reconstructed identities removed. Model structure for survival was held constant as state X time, and resight model structure was set to the best competing structure from Table S5. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. Significance of covariate effects noted in comments for competitive models.

Model	**$\Delta QAIC_c$**	**w_i**	**K**	**Comments**
$\Psi_{(\text{state X time})}$	0.00	0.42	61	
$\Psi_{(\text{manip + state X time})}$	1.12	0.24	62	Significant negative effect of manipulation
$\Psi_{(\text{cmanip + state X time})}$	1.52	0.19	62	Significant negative effect of manipulation
$\Psi_{(\text{quality + state X time})}$	2.01	0.15	62	
$\Psi_{(\text{state + time})}$	16.22	0.00	47	
$\Psi_{(\text{state X prod})}$	42.64	0.00	35	
$\Psi_{(\text{state + prod})}$	46.24	0.00	34	
$\Psi_{(\text{state + PDO})}$	55.98	0.00	34	
$\Psi_{(\text{state X PDO})}$	57.96	0.00	35	
$\Psi_{(\text{state})}$	59.54	0.00	33	
$\Psi_{(\text{time})}$	140.35	0.00	46	
$\Psi_{(\text{prod})}$	228.77	0.00	33	
$\Psi_{(\text{PDO})}$	243.86	0.00	33	
$\Psi_{(\text{constant})}$	248.63	0.00	32	

Table C8. State designation sensitivity analysis: resight probability models. Performance of multi-state models estimating the encounter probability (p) for black-legged kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010 using a criterion of two sightings on a nest sight to designate breeding status, rather than the three sightings used in the primary analysis. Model structures for survival and transition probability were held constant as state X time. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis.

Model	**$\Delta QAIC_c$**	**w_i**	**K**
$p_{(state)}$	0.00	0.98	64
$p_{(state + time)}$	8.08	0.02	79
$p_{(state \times time)}$	32.36	0.00	94
$p_{(time)}$	184.73	0.00	78
$p_{(constant)}$	228.83	0.00	63

Table C9. State designation sensitivity analysis: survival models. Performance of multi-state models estimating the probability of survival (φ) for black-legged kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010 using a criterion of two sightings on a nest sight to designate breeding status, rather than the three sightings used in the primary analysis. Model structure for transition probability was held constant as state X time, and resight model structure was set to the best competing structure from Table S8. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. Significance of covariate effects noted in comments for competitive models.

Model	**$\Delta QAIC_c$**	**w_i**	**K**	**Comments**
$\varphi_{(state + trend)}$	0.00	0.28	34	
$\varphi_{(PDO + state + trend)}$	0.03	0.27	35	Significant positive PDO effect
$\varphi_{(qual + state + trend)}$	1.58	0.13	35	Quality effect insignificant
$\varphi_{(prod + state + trend)}$	1.83	0.11	35	Productivity effect insignificant
$\varphi_{(cmanip + state + trend)}$	1.88	0.11	35	Manipulation effect insignificant
$\varphi_{(manip + state + trend)}$	1.99	0.10	35	Manipulation effect insignificant
$\varphi_{(state + time)}$	13.56	0.00	47	
$\varphi_{(state X prod)}$	13.56	0.00	35	
$\varphi_{(state X PDO)}$	13.70	0.00	35	
$\varphi_{(trend)}$	15.29	0.00	33	
$\varphi_{(state)}$	17.60	0.00	33	
$\varphi_{(state X manip)}$	19.90	0.00	35	
$\varphi_{(state X cmanip)}$	20.74	0.00	35	
$\varphi_{(time)}$	30.03	0.00	46	
$\varphi_{(state X time)}$	34.17	0.00	61	
$\varphi_{(prod)}$	40.36	0.00	33	
$\varphi_{(PDO)}$	46.26	0.00	33	
$\varphi_{(constant)}$	48.83	0.00	32	

Table C10. State designation sensitivity analysis: transition models. Performance of multi-state models estimating the probability of transition (Ψ) between breeding and non-breeding states for black-legged kittiwakes at the Shoup Bay colony, Prince William Sound, Alaska, during 1995-2010 using a criterion of two sightings on a nest sight to designate breeding status, rather than the three sightings used in the primary analysis. Model structure for survival was held constant as state X time, and resight model structure was set to the best competing structure from Table S8. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. Significance of covariate effects noted in comments for competitive models.

Model	**$\Delta QAIC_c$**	**w_i**	**K**	**Comments**
$\Psi_{(manip + state X time)}$	0.00	0.53	62	Significant negative effect of manipulation
$\Psi_{(cmanip + state X time)}$	1.37	0.27	62	Significant negative effect of manipulation
$\Psi_{(state X time)}$	2.77	0.13	61	
$\Psi_{(quality + state X time)}$	4.28	0.06	62	
$\Psi_{(state + time)}$	39.63	0.00	47	
$\Psi_{(state X prod)}$	49.26	0.00	35	
$\Psi_{(state + prod)}$	64.30	0.00	34	
$\Psi_{(state + PDO)}$	83.04	0.00	34	
$\Psi_{(state X PDO)}$	83.47	0.00	35	
$\Psi_{(state)}$	87.78	0.00	33	
$\Psi_{(time)}$	218.70	0.00	46	
$\Psi_{(PDO)}$	283.46	0.00	33	
$\Psi_{(prod)}$	312.43	0.00	33	
$\Psi_{(constant)}$	316.06	0.00	32	

Appendix D: Supplementary Information for Chapter 5

Table D1. Fledgling survival analysis: resight probability models. Performance of competing models exploring the best general structure for multistate models estimating resighting probability (p) for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony, Prince William Sound, Alaska, during 1991-2006. Asterisks denote interactive models, which include both additive and interactive effects. Model structures for survival and transition probabilities were set to general state and time dependence. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. ΔQAICc values reflect ΔAICc values adjusted according to a median ĉ estimate of 2.13.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
	Resight probability varies ...			
$p_{(state + age\ class)}$	... between breeding states and between age classes.	0.00	>0.99	57
$p_{(age\ class * year)}$	... between age classes and among years, with a different yearly pattern between age classes.	221.24	<0.01	90
$p_{(age\ class + year)}$	... between age classes and among years.	238.67	<0.01	73
$p_{(state * year)}$	... between breeding states and among years, with a different yearly pattern between breeding states.	653.54	<0.01	90
$p_{(state + year)}$	... between breeding states and among years.	693.84	<0.01	73
$p_{(state * cohort)}$	... between breeding states and among cohorts, with a different cohort pattern between breeding states.	858.14	<0.01	80
$p_{(state + cohort)}$	... between breeding states and among cohorts.	864.05	<0.01	68
$p_{(state + linear\ cohort\ trend)}$	... between breeding states and with a linear trend over cohorts.	955.15	<0.01	57
$p_{(state)}$	... between breeding states only.	969.20	<0.01	56
$p_{(cohort)}$	... among cohorts only.	1595.91	<0.01	67
$p_{(year)}$	... among years only.	1603.87	<0.01	72
$p_{(linear\ cohort\ trend)}$	... by a linear trend over cohorts only.	1729.97	<0.01	56
$p_{(constant)}$	Resight probability does not vary.	1928.83	<0.01	55

Table D2. Fledgling survival analysis: survival models. Performance of competing models exploring the best general structure for multistate models estimating the probability of apparent survival (φ; survival + fidelity) for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony, Prince William Sound, Alaska, during 1991-2008. Asterisks denote interactive models, which include both additive and interactive effects. Model structure for resight probability was set to the best competing structure (recruitment state + age class, where states were pre vs. post recruitment), and transition model structure was set to the best competing structure from transition modeling (age). Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. ΔQAICc values reflect ΔAICc values adjusted according to a median ĉ estimate of 2.13.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
	Apparent survival varies ...			
$\varphi_{(age\ class\ *\ cohort)}$	... between age classes and among cohorts, with a different cohort pattern between age classes.	0.00	>0.99	44
$\varphi_{(state\ +\ cohort)}$	... between age classes and among cohorts.	20.45	<0.01	31
$\varphi_{(age\ class\ *\ year)}$	... between age classes and among years, with a different yearly pattern between age classes.	35.74	<0.01	51
$\varphi_{(age\ +\ cohort)}$	... among ages and among cohorts.	36.60	<0.01	47
$\varphi_{(cohort\ +\ year)}$	... among cohorts and among years.	37.58	<0.01	47
$\varphi_{(age\ class\ +\ year)}$	... between age classes and among years.	48.99	<0.01	34
$\varphi_{(state\ +\ cohort)}$	... between breeding states and among cohorts.	88.14	<0.01	31
$\varphi_{(age\ *\ cohort)}$	... among ages and among cohorts, with a different age pattern among cohorts.	91.51	<0.01	140
$\varphi_{(state\ *\ cohort)}$	... between breeding states and among cohorts, with a different cohort pattern between breeding states.	106.66	<0.01	45
$\varphi_{(cohort)}$	... only among cohorts.	108.17	<0.01	30
$\varphi_{(cohort\ *\ year)}$	... among cohorts and among years, with a different yearly pattern among cohorts.	115.91	<0.01	152
$\varphi_{(state\ +\ year)}$	... between breeding states and among years.	165.51	<0.01	34
$\varphi_{(state\ *\ year)}$	... between breeding states and among years, with a different yearly pattern between breeding states.	173.99	<0.01	51
$\varphi_{(state\ +\ age\ class)}$	... between breeding states and between age classes.	201.87	<0.01	18
$\varphi_{(state\ *\ age\ classs)}$	... between breeding states and between age classes, with a different age class pattern between breeding states.	203.87	<0.01	19
$\varphi_{(age\ class)}$	... only between age classes.	205.50	<0.01	17
$\varphi_{(state\ +\ age)}$	... between breeding states and among ages.	224.51	<0.01	34
$\varphi_{(age)}$	... only among ages.	227.15	<0.01	33
$\varphi_{(state\ *\ age)}$	... between breeding states and among ages, with a different age pattern between breeding states.	247.00	<0.01	51
$\varphi_{(year)}$	... only among years.	291.85	<0.01	33
$\varphi_{(state)}$	... only between breeding states.	314.86	<0.01	17
$\varphi_{(constant)}$	Apparent survival does not vary.	400.24	<0.01	16

Table D3. Recruit survival analysis: resight probability models. Performance of competing models exploring the best general structure for multistate models estimating resighting probability (p) of post-recruitment breeders and non-breeders (determined by nest-site attendance) of Black-legged Kittiwakes banded as chicks at and eventually recruiting to the Shoup Bay colony, Prince William Sound, Alaska, during 1991-2006. Asterisks denote interactive models, which include both additive and interactive effects. Model structures for survival and transition probabilities were set to general state * time dependence. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. ΔQAICc values reflect ΔAICc values adjusted according to a median ĉ estimate of 1.76.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
	Resight probability varies ...			
$p_{(state + year)}$	... among breeding states and among years.	0.00	>0.99	105
$p_{(state + cohort)}$	... among breeding states and among cohorts.	37.14	<0.01	99
$p_{(state * year)}$	... among breeding states and among years, with a different yearly pattern of resighting probability among states.	39.95	<0.01	137
$p_{(state * cohort)}$	... among breeding states and among cohorts, with a different cohort-based pattern of resighting probability among states.	53.95	<0.01	119
$p_{(state + age)}$	... among breeding states and among ages.	60.34	<0.01	105
$p_{(state)}$	... only in relation to breeding state.	65.48	<0.01	89
$p_{(state * age)}$	... among breeding states and over age, with a different age-based pattern of resighting probability among states.	88.26	<0.01	131
$p_{(age)}$	... only by age.	216.94	<0.01	103
$p_{(year)}$	... only among years.	235.01	<0.01	103
$p_{(cohort)}$	... only by cohort.	274.86	<0.01	97
$p_{(constant)}$	Resight probability does not vary.	303.64	<0.01	87

Table D4. Recruit survival analysis: transition models. Performance of competing models exploring the best general structure for multistate models estimating the probability of state transition (ψ), where states were pre-recruitment, breeding, and post-recruitment non-breeding, for Black-legged Kittiwakes banded as chicks at and eventually recruiting to the Shoup Bay colony, Prince William Sound, Alaska, during 1991-2006. Asterisks denote interactive models, which include both additive and interactive effects. Model structure for resight probability was set to the best competing structure (breeding state + year), and survival was set to general state and time dependence. Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. ΔQAICc values reflect ΔAICc values adjusted according to a median ĉ estimate of 1.76.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
	Recruitment probability varies ...			
$\Psi_{(state * time)}$	... between breeding states and among years, with a different yearly pattern between breeding states.	0	> 0.99	104
$\Psi_{(state * age)}$	... between breeding states and among ages, with a different age pattern between breeding states.	196.73	< 0.01	98
$\Psi_{(state + age)}$	... between breeding states and among ages.	231.18	< 0.01	72
$\Psi_{(state + time)}$	... between breeding states and among years.	247.82	< 0.01	72
$\Psi_{(state + cohort)}$	... between breeding states and among cohorts.	387.35	< 0.01	72
$\Psi_{(state * cohort)}$	... between breeding states and among cohorts, with a different cohort pattern between breeding states.	395	< 0.01	98
$\Psi_{(age)}$	... among ages only.	424.71	< 0.01	70
$\Psi_{(time)}$	... among years only.	453.13	< 0.01	70
$\Psi_{(constant)}$	... does not vary.	643.58	< 0.01	54
$\Psi_{(cohort)}$	... among cohorts only.	658.32	< 0.01	70

Table D5. Recruit survival analysis: survival models. Performance of competing models exploring the best general structure for multistate models estimating the probability of apparent survival (φ; survival + fidelity) of post-recruitment breeders and non-breeders (determined by nest-site attendance) of Black-legged Kittiwakes banded as chicks at and eventually recruiting to the Shoup Bay colony, Prince William Sound, Alaska, during 1991-2006. Asterisks denote interactive models, which include both additive and interactive effects. Model structures for resight probability and transition probability were set to the best competing structure (state + time, state * time, respectively). Model weights are denoted by wi, and K represents the number of estimable parameters in each model adjusted for any parameters fixed during analysis. ΔQAICc values reflect ΔAICc values adjusted according to a median ĉ estimate of 1.76.

Model	Hypothesis	$\Delta QAIC_c$	w_i	K
	Survival probability of recruits varies ...			
$\varphi_{(state + cohort)}$	... between breeding states and among cohorts.	0	0.94	82
$\varphi_{(state)}$	... only between breeding states.	6.88	0.03	72
$\varphi_{(cohort)}$	... only among cohorts.	8.38	0.01	81
$\varphi_{(state + age class)}$	... between breeding states and between age classes.	8.93	0.01	73
$\varphi_{(state * age class)}$	... between breeding states and between age classes, with a different age pattern between breeding states.	10.98	< 0.01	74
$\varphi_{(state * cohort)}$	... between breeding states and among cohorts, with a different cohort pattern between breeding states.	13.14	< 0.01	92
$\varphi_{(constant)}$	Survival probability of recruits is constant.	15.49	< 0.01	71
$\varphi_{(age class)}$	... only between age classes.	17.53	< 0.01	72
$\varphi_{(state + year)}$	... between breeding states and among years.	19.67	< 0.01	88
$\varphi_{(state + age)}$	... between breeding states and among ages.	23.06	< 0.01	88
$\varphi_{(year)}$	... only among years.	23.11	< 0.01	87
$\varphi_{(age)}$	... only among ages.	37.05	< 0.01	87
$\varphi_{(state * year)}$	... between breeding states and among years, with a different yearly pattern between breeding states.	42.78	< 0.01	104
$\varphi_{(state * age)}$	... between breeding states and among ages, with a different age pattern between breeding states.	45.76	< 0.01	104

BIOGRAPHY OF THE AUTHOR

Aly McKnight was born in Norwich, Connecticut. Graduating from Pomfret Preparatory School in 1992, she went on to earn a Bachelor of the Arts in Zoology from Connecticut College in 1992 and a Master of Science in Wildlife and Fisheries Conservation from the University of Massachusetts - Amherst in 2000. She taught high school science at the Peddie School in Hightstown, New Jersey until 2002, spent a year teaching Biology at the Williams School in New London, CT, then worked on various seabird projects for the U.S. Fish and Wildlife Service's Office of Migratory Bird Management in Anchorage, Alaska from 2003 - 2015. Aly has authored and co-authored a number of professional reports as well as several peer-reviewed scientific journal articles. She is a member of the Pacific Seabird Group, the Ecological Society of America, and Phi Kappa Phi. She is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Sciences from the University of Maine in May 2017.